

Andrea Cau & Paolo Arduini

Enantiophoenix electrophyla gen. et sp. nov.
(Aves, Enantiornithes) from
the Upper Cretaceous (Cenomanian) of Lebanon
and its phylogenetic relationships

Abstract—The phylogenetic affinities of a new enantiornithine bird, *Enantiophoenix electrophyla* gen. et sp. nov. from the Cenomanian of Lebanon, are reviewed. It differs from other known Mesozoic birds on the basis of two scapular autapomorphies. The inclusion of *Enantiophoenix* in a phylogenetic analysis of Mesozoic birds indicates that it is a basal member of a clade of enantiornithines, Avisauridae, whose known distribution includes North America, Europe and Gondwana.

Key words: *Enantiophoenix electrophyla* gen. et sp. nov., Enantiornithes, Aves, phylogeny, Cenomanian, Lebanon.

Riassunto—*Enantiophoenix electrophyla* gen. et sp. nov. del Cretacico Superiore (Cenomaniano) del Libano e le sue relazioni filogenetiche.

In questo studio è esaminata la posizione filogenetica di un nuovo uccello enantiornite, *Enantiophoenix electrophyla* gen. et sp. nov. del Cenomaniano del Libano. Esso differisce dagli altri uccelli mesozoici noti per la presenza di due autapomorfie della scapola. L'inserimento di *Enantiophoenix* in un'analisi filogenetica degli uccelli mesozoici mostra che esso è un rappresentante basale di un clade di enantiorniti, Avisauridae, la cui distribuzione nota attualmente abbraccia Nord America, Europa e Gondwana.

Parole chiave: *Enantiophoenix electrophyla* gen. et sp. nov., Enantiornithes, Aves, filogenesi, Cenomaniano, Libano.

Introduction

Dalla Vecchia & Chiappe (2002) reported an avian specimen from the Upper Cretaceous of Lebanon and referred it to the clade Enantiornithes Walker (1981). This specimen (MSNM V3882, Vertebrate Paleontological Collection of the Museo di Storia Naturale di Milano) is palaeogeographically very important as it is the first record of a Mesozoic bird from northern Gondwana, however, its exact phyloge-

netic position was not discussed in details. After further preparation and study, it has been established that MSNM V3882 is different from other known enantiornithines based on a unique combination of features (Nixon & Wheeler, 1990) and two autapomorphies.

Institutional acronyms: CAGS, Chinese Academy of Geological Sciences, Beijing (China); MSNM, Museo di Storia Naturale di Milano (Italy).

Anatomical abbreviations: **ac**, acetabulum; **acr**, acrocoracoid; **fe**, feathers; **lc**, left coracoid, **lsc**, left scapula; **mti**, insertion of the *Musculus tibialis cranialis*; **pf**, pedal phalanges; **pu**, pubis; **rc**, right coracoid; **tm**, right tarsometatarsus; **sac**, scapular acromion; **snf**, foramen of the supracoracoid nerve; **st**, sternum.

Systematic Palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Aves Linnè, 1758

Ornithothoraces Chiappe & Calvo, 1994

Enantiornithes Walker, 1981

Euenantiornithes Chiappe, 2002

Avisauridae Brett-Surman & Paul, 1985

Definition (emended): Avisauridae is here defined as the most inclusive clade containing *Avisaurus archibaldi* Brett-Surman & Paul, 1985, but not *Sinornis sanctensis* Sereno & Rao, 1992, *Gobipteryx minuta* Elzanowski, 1974, or *Longipteryx chaoyangensis* Zhang *et al.*, 2001.

Comments: Chiappe (1993: 14) published the first phylogenetic definition of the clade as “the common ancestor of *Neuquenornis volans* and *Avisaurus archibaldi* plus all its descendants”; yet he did not point out that the ancestor is the most recent one shared by the two species. T (this is the definition of a common ancestor, “most recent” is implied. Though I agree those words should have been included for absolute clarity, I am not sure this is necessary his definition is ambiguous because it does not specify the inclusiveness of the clade. Given that the enantiornithine relationships are not well resolved (Sereno *et al.*, 2002), we suggest using a definition that explicitly mentions only *Avisaurus* as a member of the family and, at the same time, excludes the three well-known species of enantiornithines cited above from Avisauridae. The aim of the latter statement is to preserve the mutual exclusiveness of the names Avisauridae, Gobipterygidae, Longipterygidae and Sinornithidae (the latter regarded as a synonym of Cathayornithidae) among the different phylogenetic hypotheses that could be proposed.

Enantiophoenix gen. nov.

Enantiophoenix electrophyla sp. nov.

Etymology: The generic name (Greek: “the opposite phoenix”) refers to the enantiornithine status of MSNM V3882 (Dalla Vecchia & Chiappe, 2002; see below) and to the mythological bird “Phoenix”, which alludes to the ancient name

of Lebanon. The specific name (Greek: “that likes amber”) refers to the presence of amber corpuscles scattered between its bones (Dalla Vecchia & Chiappe, 2002).

Holotype: MSNM V3882a and b [MSNM V3882a, larger slab (Fig. 1), and b, smaller slab] is an incomplete and disarticulated skeleton mixed with carbonized remains of feathers (Dalla Vecchia & Chiappe, 2002). Most of the elements (pectoral girdle, sternum, pelvic bones, metatarsals and pedal phalanges) are preserved in the larger slab, while the smaller is a partial counterpart of the larger.

Locality and Horizon: Left flank of the Ouadi al Gabour near the village of Nammoûra (Kesrouâne Caza, Mohafazat of Mont-Liban), some 25 km NE of Beirut. Late middle Cenomanian (Dalla Vecchia & Venturini, 1999).

Diagnosis: An enantiornithine bird that differs from other known taxa in that its scapular blade is somewhat constricted proximally with a short and low acromion that is not very projected cranially (Fig. 2). It differs from *Protopteryx* (Zhang & Zhou, 2000) by lacking a procoracoid process of the coracoid; from *Elsornis* (Chiappe *et al.*, 2006) by the presence of an acrocoracoid tubercle (Chiappe & Walker, 2002) and by the absence of a kinked dorsal margin of the scapular blade; from *Longipteryx* (Zhou *et al.*, 2001), and *Boluochia* (Zhou, 1995) in that the metatarsal II is shorter than metatarsal III; from *Longirostravis* (Hou *et al.*, 2004) in that the tarsometatarsus is longer than 4/3 of the coracoid (in *Longirostravis* the tarsometatarsus is about as long as the coracoid); from *Eoenantiornis* (Hou *et al.*, 1999) and *Eocathayornis* (Zhou, 2002) in that the coracoid is relatively slender and elongate; from *Eoalulavis* (Sanz *et al.*, 1996) and *Gobipteryx* (Elzanowski, 1974, with *Nanantius valifanovi* Kurochkin, 1996, as junior synonym of *Gobipteryx minuta* Elzanowski, 1974, according to Chiappe *et al.*, 2001) by the absence of an extremely slender coracoid (Chiappe & Walker, 2002); from *Halimornis* (Chiappe *et al.*, 2002), *Neuquenornis* (Chiappe & Calvo, 1994) and *Enantiornis* (Walker, 1981) by the absence of a longitudinal groove on the costal surface of the scapula; from *Soroavisaurus* (Chiappe, 1993) by the absence of a wide metatarsal fenestra; from *Avisaurus* (Brett-Surman & Paul, 1985) by its more gracile tarsometatarsus and its less developed and more proximally placed tubercle on the metatarsal II; from *Yungavolucris* and *Lectavis* (Chiappe, 1993) by the presence of a more medially placed insertion of the *Musculus tibialis cranialis* on the metatarsal II; from *Concornis* (Sanz & Buscalioni, 1992) in having a more rounded (“U”-shaped) furcula; and from *Iberomesornis* (Sanz & Bonaparte, 1992), *Dalingheornis* (Zhang *et al.*, 2006), *Sinornis* (Serenó & Rao, 1992) [with *Cathayornis* regarded as a junior synonym by Sereno *et al.*, (2002)] and *Vescornis* (Zhang *et al.*, 2004) by its relatively thicker first phalanx of first pedal digit. The unnamed enantiornithines CAGS-IG-02-0901 (You *et al.*, 2005) and CAGS-IG-04-CM-007 (Lamanna *et al.*, 2006) cannot be referred to *Enantiophoenix* because they lack, respectively, the scapular autapomorphies and the marked curvature of the pedal unguals of the Lebanese form.

Description and comparison

This description is aimed to supplement the anatomical description provided by Dalla Vecchia & Chiappe (2002). Therefore, it includes only previously overlooked details and characters that were useful in determining the taxonomic status of *Enantiophoenix*. The phylogenetically most informative characters are preserved in the larger slab, and pertain to the pectoral girdle and the *pes*.

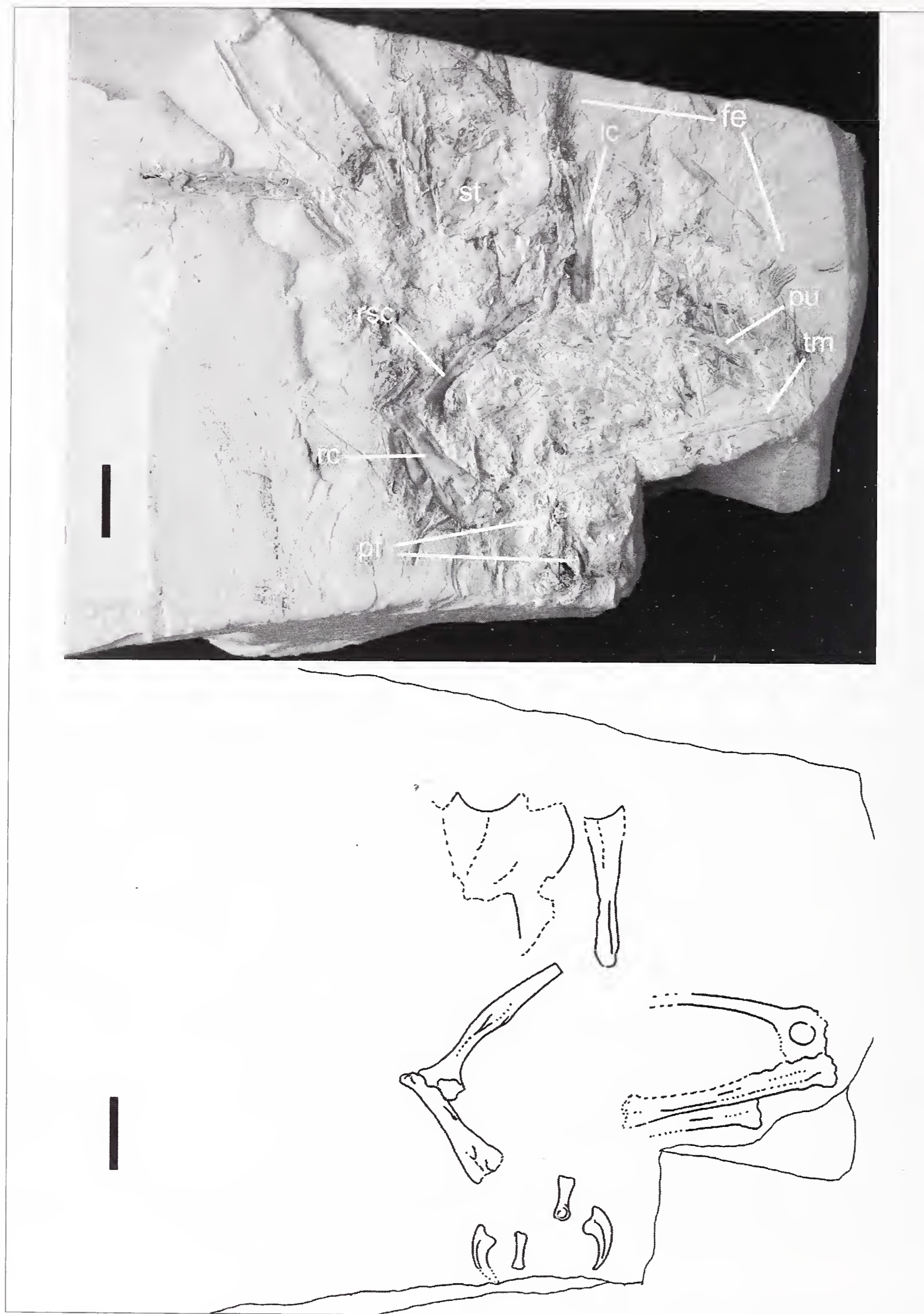


Fig. 1 - *Enantiophoenix electrophyla* gen. et sp. nov. Holotype, larger slab (MSNM V3882a). Abbreviations: fe, feathers; lc, left coracoid, pf, pedal phalanges; pu, pubis; rc, right coracoid; rsc, right scapula; tm, right tarsometatarsus; st, sternum. Scale bar equals 10 mm.

Fig. 1 - *Enantiophoenix electrophyla* gen. et sp. nov. Olotipo, lastra maggiore (MSNM V3882a). Abbreviazioni: fe: piumaggio, lc, coracoide sinistro; pf, falangi del piede; pu, pube; rc, coracoide destro; rsc, scapola destra; tm, tarsometatarso destro; st, sterno. La scala metrica equivale 10 mm.

Pectoral girdle (Fig. 2). The strut-like coracoid (length 19.4 mm) is elongate and slender, about three times as long (length measured between the scapular and the sternal ends) as its distal width. This proportion is similar in *Sinornis* (Sereno *et al.*, 2002) and *Vescornis* (Zhang *et al.*, 2004), and intermediate between the relatively shorter and stouter coracoids of *Eocathayornis* and *Eoenantiornis* (Zhou, 2002), and the even more elongate and slender coracoids of *Gobipteryx* and *Eoalulavis* (Chiappe & Walker, 2002). A small tubercle is present between the proximo-medial margin of the acrocoracoid process and the humeral articular surface, similar to the condition found in *Enantiornis* (Chiappe & Walker, 2002), but not in *Elsornis* (Chiappe *et al.*, 2006). The foramen of the supracoracoid nerve is separated from the medial margin of the coracoid by a cylindrical bar of bone, a condition shared with most enantiornithines (Chiappe & Calvo, 1994). A coracoidal dorsal fossa is not visible, yet its presence is inferred on the basis of the collapsed sternal half of the coracoid (Dalla Vecchia & Chiappe, 2002). Unfortunately, both coracoids are preserved in ventral view, making it impossible to determine whether the supracoracoid foramen opens above the coracoidal dorsal fossa as in *Gobipteryx*, *Enantiornis* and *Sinornis*, or inside it, as in *Neuquenornis* (Chiappe & Walker, 2002). As in most enantiornithines, the sternal third of the lateral margin of the coracoid is convex. The scapula of *Enantiophoenix* (length 21.3 mm) is unique among the known Mesozoic birds; the scapular shaft is somewhat dorso-ventrally depressed between the acromial region and the distal half (Fig. 2). In other enantiornithines the same region is typically as thick (Walker, 1981; Chiappe *et al.*, 2002; Zhou, 2002) or thicker (Chiappe *et al.*, 2006) than the middle of the blade (Fig. 4B-E). The acromion is low, without a distinct neck, less prominent and less steeply rising than in other enantiornithines (Walker, 1981; Kurochkin, 1996; Chiappe & Walker, 2002; Zhang *et al.*, 2004; Chiappe *et al.*, 2006; Lamanna *et al.*, 2006); a condition shared by *Eocathayornis* (Zhou, 2002; O'Connor, pers. com., 2008; Fig. 4D). The Lebanese taxon differs from *Eocathayornis* (and other enantiornithines) because its acromion is not very projected cranially. In other taxa (Zhou, 2002; Zhang *et al.*, 2004; Chiappe *et al.*, 2006; Lamanna *et al.*, 2006) the acromion is craniodorsally directed, having the distal tip that projects beyond the level of the scapular glenoid (Fig. 4B-E), a condition shared by most paravian theropods (Norell & Makovicky, 1999). The proximal quarter of the scapula is distinctly ventrally bent, a condition shared by *Elsornis* (Chiappe *et al.*, 2006) too. The costal surface is slightly depressed though it lacks the longitudinal groove reported in *Enantiornis*, *Halimornis* and *Neuquenornis* (Chiappe *et al.*, 2002).

Pes. The metatarsals II-IV are proximally fused with the distal tarsals to form a tarsometatarsus, as in living birds and some other theropods (Fig. 3). The right tarsometatarsus is preserved better than the left one (estimated length, 28 mm) and in it the third metatarsal is more collapsed than the second. This may indicate that the tarsometatarsus was plantarly excavated, as in *Lectavis* and avisaurids (Chiappe, 1993). The tarsometatarsus is stouter than in *Neuquenornis* and *Lectavis* (Chiappe, 1993), with a length/width ratio of about 6.5, a condition similar to those of other basal birds (Chiappe & Calvo, 1994), but relatively thinner than those of *Avisaurus*, *Soroavisaurus* and *Yungavolucris* (Chiappe, 1993; Chiappe & Calvo, 1994). As reported by Dalla Vecchia & Chiappe (2002), the medial margin of metatarsal II bears a proximal swell, possibly for the insertion of *Musculus tibialis cranialis* (Chiappe, 1993; Norell and Makovicky, 1997). The position of this insertion, along the medial margin of metatarsal II, better recalls that observed in *Soroavisaurus* and *Avisaurus* (Fig. 4J-K; Chiappe, 1993) rather than in other enantiornithines (for

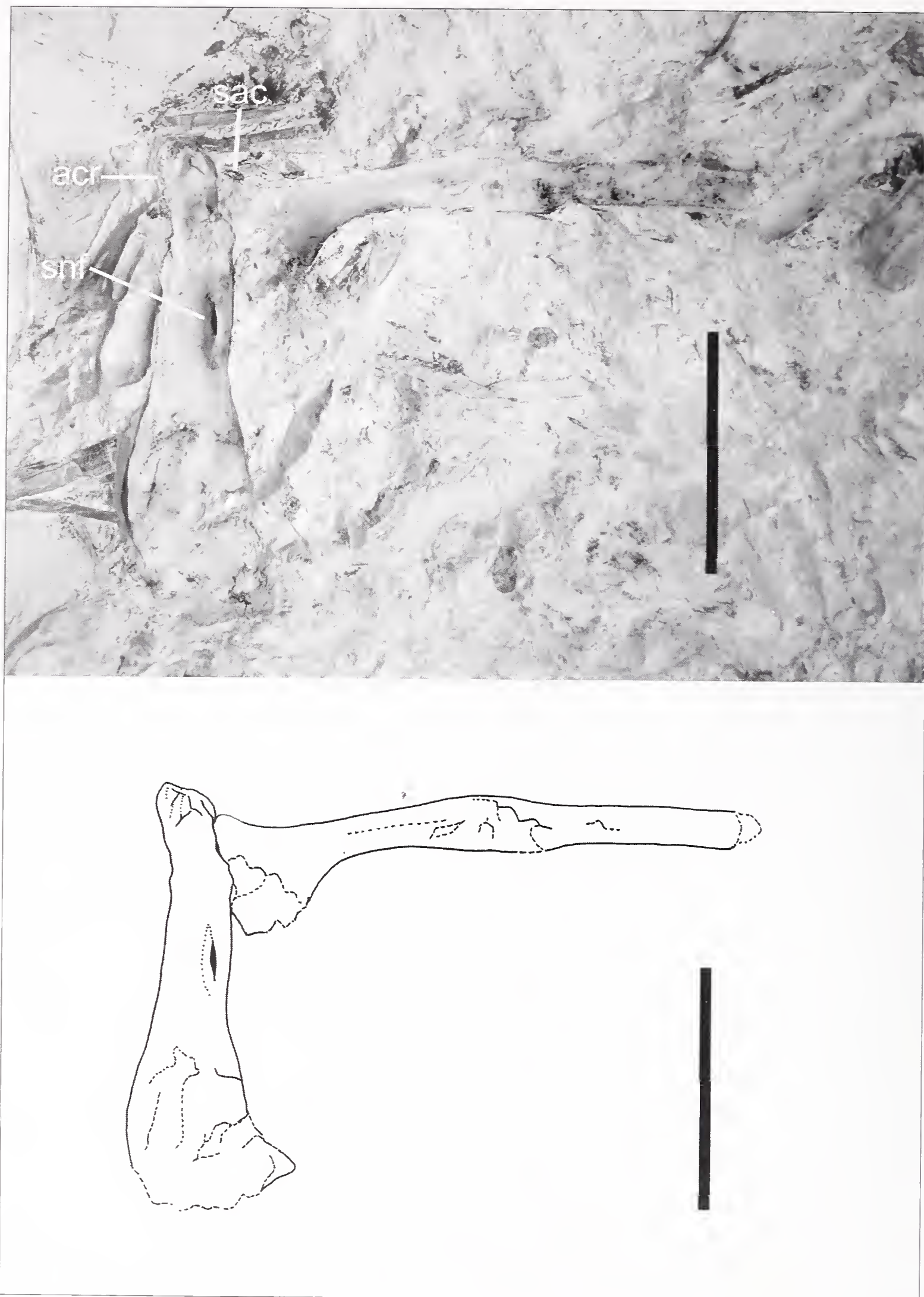


Fig. 2 - *Enantiophoenix electrophyla* gen. et sp. nov. Holotype, larger slab (MSNM V3882a). Right scapula in costal view and right coracoid in ventral view. Abbreviations: acr, acrocoracoid; sac, scapular acromion; snf, foramen of the supracoracoid nerve. Scale bar equals 10 mm.

Fig. 2 - *Enantiophoenix electrophyla* gen. et sp. nov. Olotipo, lastra maggiore (MSNM V3882a). Scapola destra in vista costale e coracoide destro in vista ventrale. Abbreviazioni: acr, acrocoracoide; sac, acromion della scapola; snf, forame del nervo sopracoracoideo. La scala metrica equivale a 10 mm.

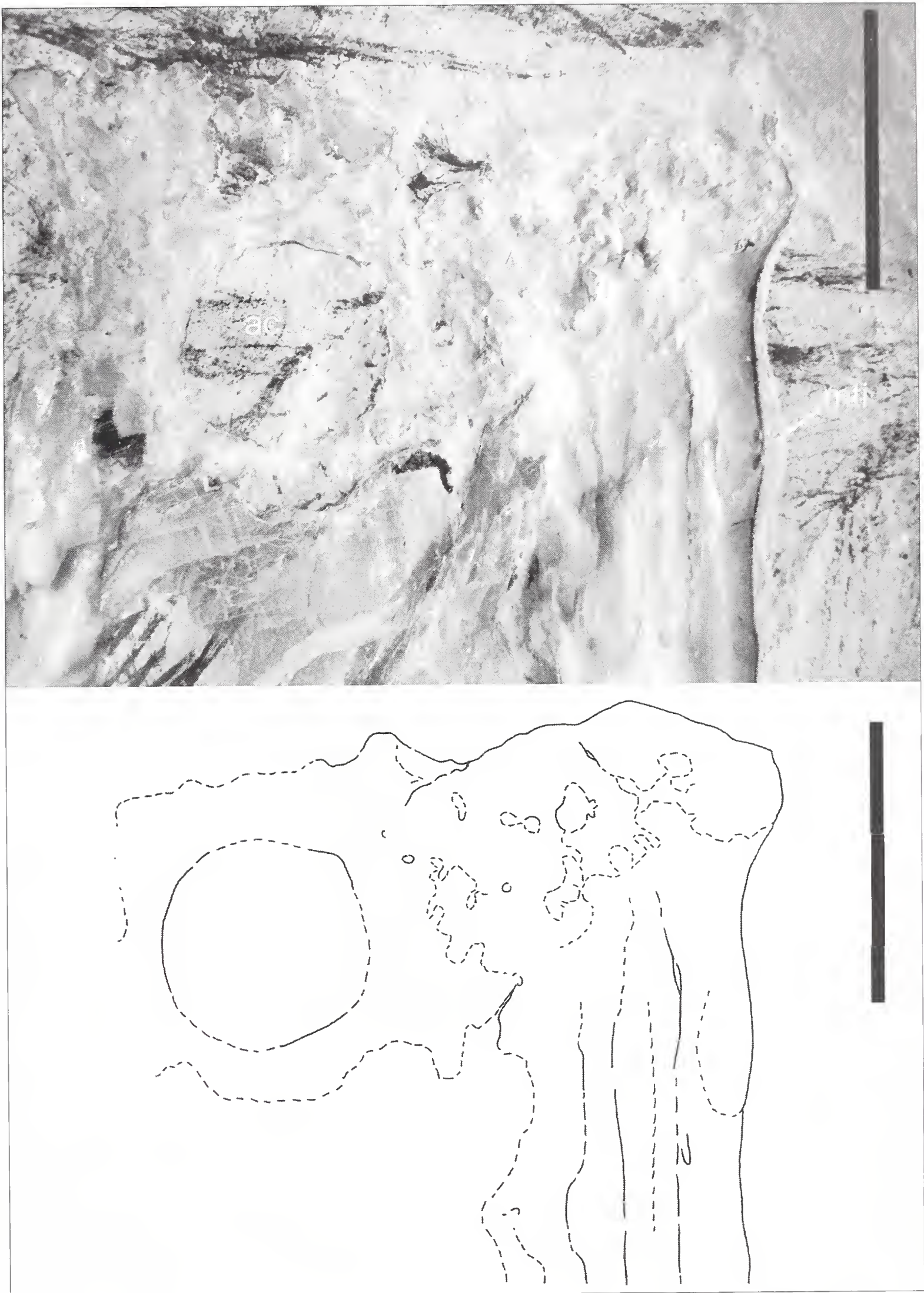


Fig. 3 - *Enantiophoenix electrophyla* gen. et sp. nov. Holotype, larger slab (MSNM V3882a). Proximal end of the right tarsometatarsus in extensor view. Abbreviations: ac, acetabulum; mti, insertion of the *Musculus tibialis cranialis*. Scale bar equals 5 mm.

Fig. 3 - *Enantiophoenix electrophyla* gen. et sp. nov. Olotipo, lastra maggiore (MSNM V3882a). Regione prossimale del tarsometatarso destro in vista estensoria. Abbreviazioni: ac, acetabolo; mti, inserzione del *Musculus tibialis cranialis*. La scala metrica equivale a 5 mm.

example in *Lectavis* and *Yungavolucris*, Chiappe, 1993; or in *Gobipteryx*, Kurochkin, 1996), which bear a more centrally located tubercle on metatarsal II (Fig. 4G-H). Although poorly preserved, metatarsal II is clearly shorter than III and distally straight, lacking the strong distal twist observed in more derived avisaurids (Chiappe, 1993). Metatarsals III and IV are badly preserved. At mid-length, metatarsal III is 120% broader than metatarsal II. Metatarsal IV is narrower than both metatarsals II and III, being about half the width of metatarsal III. Several pedal phalanges are preserved and partially in articulation. We follow Dalla Vecchia & Chiappe (2002), and consider the stoutest of the preserved phalanges, associated

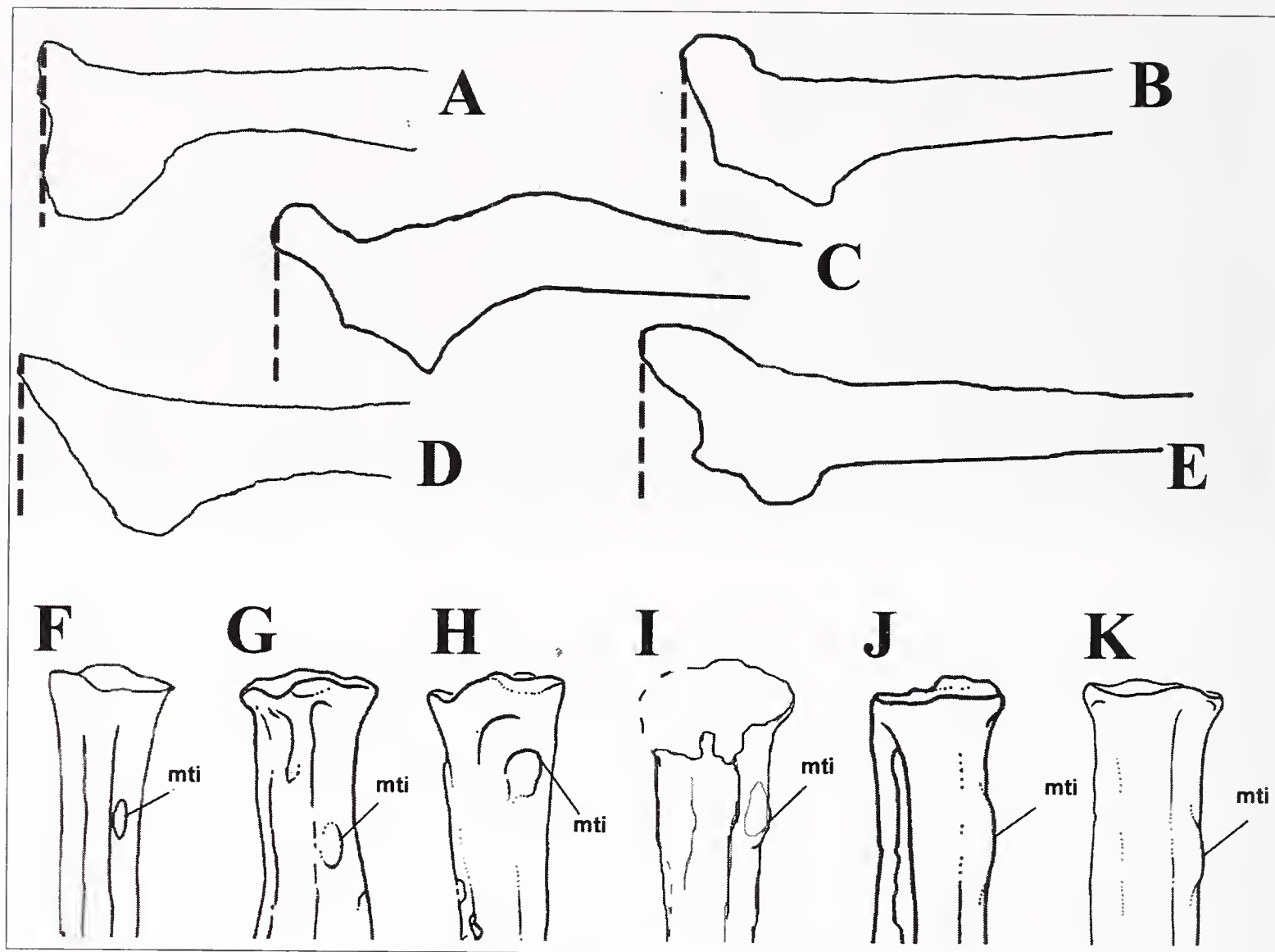


Fig. 4 - Basal avialan proximal scapulae and tarsometatarsi. A-E) proximal end of scapulae in costal (medial) view. A) *Enantiophoenix* (this study). B) *Halimornis* (modified from Chiappe *et al.*, 2002). C) *Elsornis* (modified from Chiappe *et al.*, 2006). D) *Eocathayornis* (modified from Zhou, 2002). E) *Enantiornis* (modified from Walker, 1981). The broken lines mark the level of the cranial end of the acromion. F-K) proximal end of right tarsometatarsi in extensor view. F) *Confuciusornis* (modified from Chiappe *et al.*, 1999). G) *Yungavolucris* (modified from Chiappe, 1993). H) *Lectavis* (modified from Chiappe, 1993). I) *Enantiophoenix* (this study). J) *Soroavisaurus* (modified from Chiappe, 1993). K) *Avisaurus* (modified from Chiappe, 1993). Abbreviations: mti, insertion of the *Musculus tibialis cranialis*. Figures not to scale.

Fig. 4 - Regione prossimale della scapola e del tarsometatarso di aviali basali. A-E) apice prossimale della scapola in vista costale (mediale). A) *Enantiophoenix* (questo studio). B) *Halimornis* (modificato da Chiappe *et al.*, 2006). C) *Elsornis* (modificato da Chiappe *et al.*, 2006). D) *Eocathayornis* (modificato da Zhou, 2002). E) *Enantiornis* (modificato da Walker, 1981). Le linee tratteggiate indicano il livello craniale dell'acromion. F-K) regione prossimale del tarsometatarso destro in vista estensoria. F) *Confuciusornis* (modificato da Chiappe *et al.*, 1999). G) *Yungavolucris* (modificato da Chiappe, 1993). H) *Lectavis* (modificato da Chiappe, 1993). I) *Enantiophoenix* (questo studio). J) *Soroavisaurus* (modificato da Chiappe, 1993). K) *Avisaurus* (modificato da Chiappe, 1993). Abbreviazioni: mti, inserzione del *Musculus tibialis cranialis*. Figure non in scala.

with a broad ungual near its distal articulation, as pedal digit I. The proximal phalanx is relatively stouter than that of *Iberomesornis* (Sanz & Bonaparte, 1992, MSNM V3642), *Sinornis* (Sereno *et al.*, 2002) and *Vescornis* (Zhang *et al.*, 2004), but similar to the condition observed in *Concornis* (Sanz *et al.*, 1995, MSNM V3643) and *Neuquenornis* (Chiappe & Calvo, 1994). As in *Soroavisaurus* and *Neuquenornis*, the distal articular surface of this phalanx is expanded and bears well developed collateral fossae. The preserved pedal unguals are more ventrally curved (which direction is the curvature?) than those of *Iberomesornis* (Chiappe & Walker, 2002, MSNM V3642), *Elsornis*, *Gobipteryx* and CAGS-IG-04-CM-007, and similar to the condition found in *Sinornis*, *Vescornis* and *Boluochia*.

Phylogenetic analysis

In order to determine the phylogenetic position of *Enantiophoenix*, we incorporated the anatomical information obtained from MSNM V3882 into a data matrix for a phylogenetic analysis of basal avialan (*sensu* Gauthier, 1986) interrelationships. The analysis includes 34 pygostylian (*sensu* Gauthier & de Queiroz, 2001) operative taxonomic units (OTUs) in the ingroup (33 generic-level OTUs and the suprageneric taxon Neornithes) and 2 outgroups (*Archaeopteryx* and *Jeholornis*), coded for 192 characters. Analyses were carried out in PAUP* 4.0b10 (Swofford, 2002); all characters were treated as equally weighted and 50 characters are ordered (see Appendix 1 and 2). Analysis was carried out using a heuristic search with 1000 replicates and TBR branch-swapping, each starting tree being produced by random stepwise addition.

Results

Our analysis found a single most parsimonious tree (MPT) of 629 steps (CI = 0.5246; RI = 0.6215), as shown in Fig. 5.

Enantiophoenix is resolved within Enantiornithes, the most diverse and widespread clade of Cretaceous birds. Our analysis shows that *Iberomesornis* is the most basal known enantiornithine, a conclusion in agreement with other previous works (Sereno, 2000; Chiappe, 2002; You *et al.*, 2005; *contra* Chiappe & Calvo, 1994; Sanz *et al.*, 1995). The remaining enantiornithines form Euenantiornithes (Chiappe, 2002). *Protopteryx*, *Elsornis*, *Dalingheornis* and *Eoalulavis* are in sequence closer sister-groups of a series of suprageneric clades of derived enantiornithines. Our analysis found a clade comprising *Gobipteryx*, *Boluochia* and *Vescornis*. It also establishes a large clade that includes *Longipteryx*, *Longirostravis* (Hou *et al.*, 2004), *Eoenantiornis* (forming a monophyletic clade also in the analysis of Chiappe *et al.*, 2007), and the unnamed enantiornithines CAGS-IG-02-0901 (You *et al.*, 2005) and CAGS-IG-04-CM-007 (Lamanna *et al.*, 2006), all from the Early Cretaceous of China. *Eocathayornis* and *Sinornis* are in sequence the closest sister-groups of Avisauridae. *Enantiophoenix* is resolved as the basalmost avisaurid. It shares with more derived avisaurids the presence of a hypertrophied first phalanx of pedal digit I and the presence of a medially placed insertion for the *Musculus tibialis cranialis* on the metatarsal II. The absence of the grooved costal surface of the scapula places *Enantiophoenix* outside the clade formed by *Halimornis*, *Concornis*, *Neuquenornis*, *Avisaurus* and *Soroavisaurus*. The relationships among avisaurids more derived than *Halimornis* agree with those found by previous studies (Chiappe, 1993; Sanz *et al.*, 1995) and are not discussed here.

Phylogenetic relationships within the enantiornithine clade are still poorly resolved (Chiappe 2002; Chiappe and Walker 2002; Sereno *et al.* 2002; Chiappe *et al.*, 2007). In order to test the robustness of found clades, the same software used in the phylogenetic analysis was used to determine the Decay Index of the nodes of the MPT, and to run bootstrap and jackknife analyses, using in both tests 100 random addition-sequence replicates with “maxtrees” set at 1000. The Bremer, bootstrap and jackknife supports are weak in most of the nodes (Tab. 1). Only the whole ingroup, the node Ornithothoraces and the euornithine clades more derived than *Archaeorhynchus* result with bootstrap and jackknifes values greater than 50%.

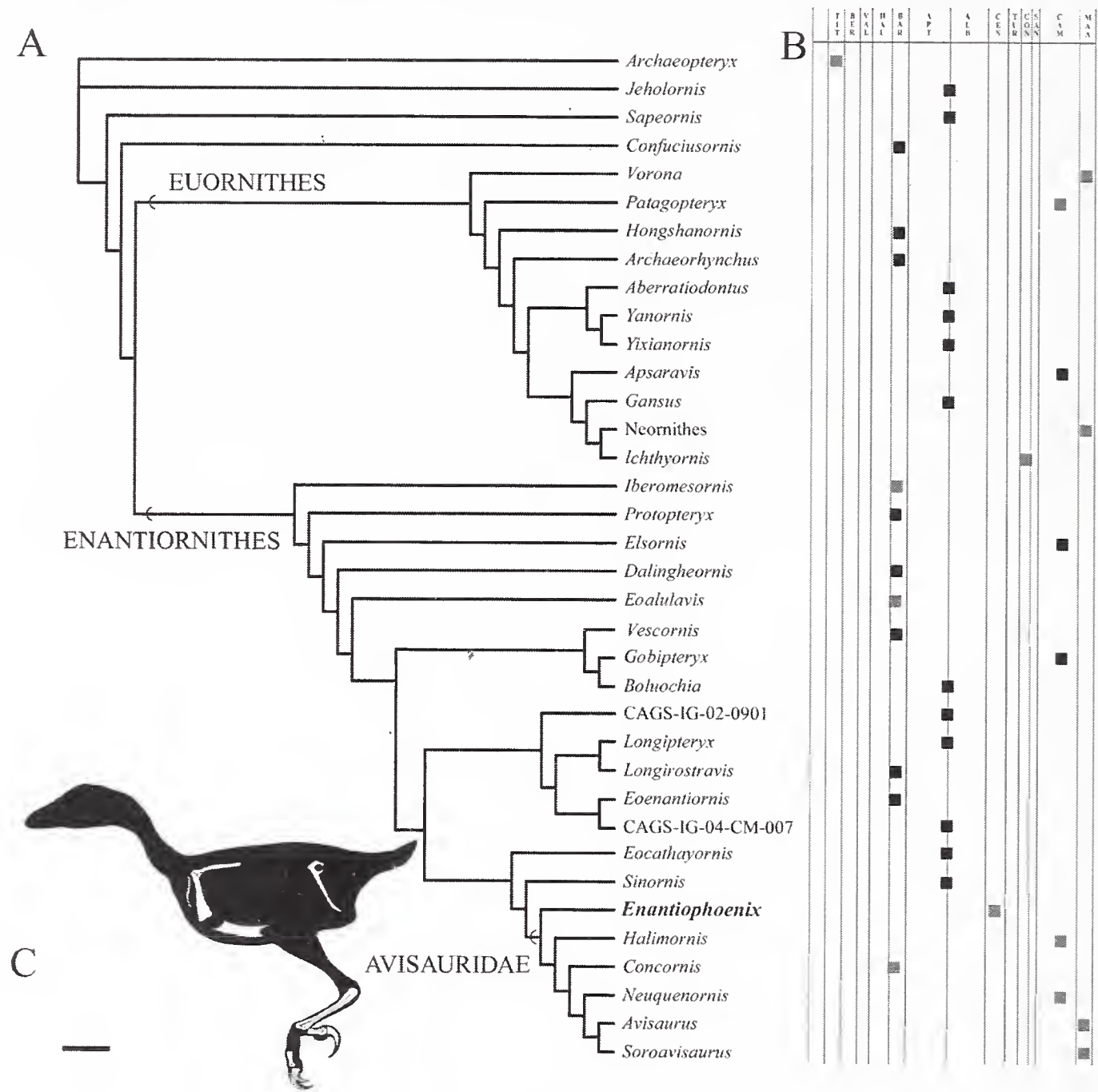


Fig. 5 - Phylogeny within Mesozoic avialans. A) cladogram depicting the phylogenetic position of *Enantiophoenix* based on the phylogenetic analysis discussed in the text. B) geochronological distribution of the taxa included in the phylogenetic analysis (Chiappe & Dyke, 2002). Black squares denote Asian taxa, grey squares denote non-Asian taxa. C) silhouette reconstruction of an enantiornithine showing the preserved remains of MSNM V3882 discussed in the text. Abbreviations: TIT, Tithonian; BER, Berriasian; VAL, Valanginian; HAU, Hauterivian; BAR, Barremian; APT, Aptian; ALB, Albian; CEN, Cenomanian; TUR, Turonian; CON, Coniacian; SAN, Santonian; CAM, Campanian; MAA, Maastrichtian. Scale bar equals 20 mm.

Fig. 5 - Filogenesi degli aviali mesozoici. A) cladogramma illustrante la posizione filogenetica di *Enantiophoenix* sulla base dell'analisi filogenetica discussa nel testo. B) distribuzione geocronologica dei taxa inclusi nell'analisi filogenetica (Chiappe & Dyke, 2002). I quadrati neri denotano taxa asiatici, i quadrati grigi denotano taxa non-asiatici. C) sagoma di enantiornite mostrante i resti preservati di MSNM V3882 discussi nel testo. Abbreviazioni: TIT, Titoniano; BER, Berriasiano; VAL, Valanginiano; HAU, Hauteriviano; BAR, Barremiano; APT, Aptiano; ALB, Albiano; CEN, Cenomaniano; TUR, Turoniano; CON, Coniaciano; SAN, Santoniano; CAM, Campaniano; MAA, Maastrichtiano. La scala metrica equivale a 20 mm.

Tab. 1 - Synapomorphies under delayed character-state optimisation, Bremer Support (B. S.) in number of steps, jackknife value (J%) and bootstrap value (B%) supporting each node of the MPT.

Tab. 1 - Sinapomorfie sotto l’ottimizzazione decelerata dello stato dei caratteri, valore di Bremer Support (B. S.) in numero di “steps”, valore di “jackknife” (J%) e del “bootstrap” (B%), a supporto dei nodi del MPT.

Node (The clade notation used below, “taxon A + taxon B”, refers to the least inclusive clade in the MPT comprising the two given taxa. It does not imply that these taxa share a direct sister-taxon relationship).	Character states supporting the node under Deltran optimisation (See Appendix 1 for a description of the character states. Unambiguous apomorphies in bold).	B. S.	J%	B%
<i>Sapeornis</i> + Neornithes	3.1; 13.1; 23.1; 34.1 ; 35.2; 39.1 ; 56.5 ; 60.0 ; 61.1 ; 63.1 ; 90.1 ; 104.1; 113.1 ; 128.2 ; 181.1	4	79	96
<i>Confuciusornis</i> + Neornithes	6.1 ; 8.2 ; 11.1; 14.2; 18.1; 59.4; 73.0; 76.2 ; 79.2; 92.1 ; 111.0 ; 118.1; 130.1 ; 152.1 ; 159.1; 162.1; 168.1 ; 169.1; 173.1	3	<50	< 50
Enantiornithes + Euornithes	20.2 ; 46.1 ; 54.1 ; 65.3; 66.1; 87.1 ; 96.1 ; 97.3; 115.2; 116.2 ; 122.2 ; 127.1 ; 133.0 ; 147.0 ; 160.2; 189.0 ; 191.1	2	63	63
<i>Vorona</i> + Neornithes	161.2 ; 166.0 ; 167.1	2	< 50	< 50
<i>Patagopteryx</i> + Neornithes	26.1; 89.0; 134.0; 139.0; 146.1; 150.0; 157.1; 163.1 ; 186.1; 190.1	2	< 50	< 50
<i>Hongshanornis</i> + Neornithes	3.2; 5.1; 19.1; 21.1; 53.1 ; 62.0; 72.1 ; 82.1 ; 109.1; 125.1; 146.0	2	< 50	< 50
<i>Archaeorhynchus</i> + Neornithes	14.0 ; 41.1; 73.1 ; 113.2 ; 118.3; 128.1 ; 155.2; 187.0	2	< 50	< 50
<i>Yanornis</i> + Neornithes	28.1; 29.2; 39.0 ; 54.2; 56.7; 91.1; 105.1; 108.0; 112.2 ; 115.3; 119.1 ; 126.0; 135.1 ; 159.2; 172.1 ; 183.1	3	67	63
<i>Aberratiodontus</i> + <i>Yanornis</i>	5.0 ; 11.0; 31.1; 34.0 ; 35.1 ; 83.2 ; 120.1; 121.2	2	65	56
<i>Yanornis</i> + <i>Yixianornis</i>	37.1 ; 98.0; 123.1 ; 124.2	2	72	62
<i>Apsaravis</i> + Neornithes	45.0; 56.8 ; 98.2; 99.1; 140.1 ; 141.1; 151.2 ; 173.0; 188.0	3	73	70
<i>Gansus</i> + Neornithes	49.1; 55.1; 57.2 ; 58.1 ; 101.0; 105.2; 106.2; 110.0; 117.0; 135.0 ; 158.1	1	53	51
<i>Ichthyornis</i> + Neornithes	24.1; 25.1; 27.1; 47.2; 50.1 ; 75.2 ; 76.0; 96.2 ; 102.0 ; 107.0 ; 169.0; 182.1	1	56	63
<i>Iberomesornis</i> + <i>Avisaurus</i>	71.1 ; 118.2; 128.3 ; 154.2; 155.0 ; 184.3	3	< 50	< 50
<i>Protopteryx</i> + <i>Avisaurus</i>	33.1; 34.0; 108.0; 114.0; 129.1; 175.1; 176.1	1	< 50	< 50

<i>Elsornis</i> + <i>Avisaurus</i>	44.0; 77.1; 81.1; 82.2; 91.1; 94.1; 113.0; 126.0	1	< 50	< 50
<i>Dalingheornis</i> + <i>Avisaurus</i>	11.0; 56.6; 189.1	1	< 50	< 50
<i>Eoalulavis</i> + <i>Avisaurus</i>	52.1; 74.1; 76.1; 78.1; 80.2; 86.1; 105.1; 106.2; 115.3; 125.1	1	< 50	< 50
<i>Gobipteryx</i> + <i>Avisaurus</i>	9.0; 17.0; 101.0; 110.0; 124.1; 138.2; 145.1; 155.1; 156.1; 157.1; 159.2; 171.0; 190.1	1	< 50	< 50
<i>Vescornis</i> + <i>Gobipteryx</i>	165.1; 166.0	1	< 50	< 50
<i>Gobipteryx</i> + <i>Boluochia</i>	3.2; 5.1; 164.1	1	< 50	< 50
<i>Longipteryx</i> + <i>Avisaurus</i>	13.0; 24.1; 67.1; 123.1	1	< 50	< 50
CAGS-IG-02-0901 + <i>Longipteryx</i>	111.1; 113.1	1	< 50	< 50
<i>Eoenantiornis</i> + <i>Longipteryx</i>	53.1; 80.1	1	< 50	< 50
<i>Eoenantiornis</i> + CAGS-IG-04-CM-007	140.1; 160.1; 189.0	1	< 50	< 50
<i>Longipteryx</i> + <i>Longirostravis</i>	1.2; 11.1; 31.1; 32.1; 175.0	1	< 50	< 50
<i>Eocathayornis</i> + <i>Avisaurus</i>	23.0; 105.2	1	< 50	< 50
<i>Sinornis</i> + <i>Avisaurus</i>	126.1; 169.0; 174.1	1	< 50	< 50
<i>Enantiophoenix</i> + <i>Avisaurus</i>	167.2; 185.2	1	< 50	< 50
<i>Halimornis</i> + <i>Avisaurus</i>	47.2; 70.1; 91.2	1	< 50	< 50
<i>Concornis</i> + <i>Avisaurus</i>	153.1; 172.2	1	< 50	< 50
<i>Neuquenornis</i> + <i>Avisaurus</i>	180.1	1	< 50	< 50
<i>Avisaurus</i> + <i>Soroavisaurus</i>	165.1	1	< 50	< 50

Discussion

Although *Enantiophoenix* is based on a fragmentary specimen, it displays a combination of features that support its avian and enantiornithine assignment (presence of a strut-like coracoid bearing the scapular articulation below the shoulder end, presence of a supracoracoid nerve foramen of the coracoid separated from the medial margin by a bar of bone, presence of proximally fused tarsometatarsus, presence of a slender metatarsal IV, inferred presence of a retroverted hallux; Dalla Vecchia & Chiappe, 2002).

We considered the hypothesis that the low and short acromion with little cranial projection seen in MSNM V3882 could be a juvenile character and not an autapomorphy. MSNM V3882 lacks the intensive scarring of pits and grooves on the periosteal surface of the bones seen in juvenile enantiornithines (Sanz *et al.*, 1997; Chiappe *et al.*, 2007), and has the large sternum (Dalla Vecchia & Chiappe, 2002; Fig. 1) and completely fused tarsometatarsus, associated with mature individuals. Regardless of their ontogenetic stage, juvenile enantiornithines, whose scapulae are known, share with adult enantiornithines, with the exception of *Enantiophoenix* and *Eocathayornis* (see above), an elongate and robust acromion (Chiappe *et al.*, 2007). Therefore, we consider the morphology of the scapular acromion of MSNM V3882 as an apomorphy of a new enantiornithine species.

The position of the proximal tubercle on metatarsal II and the presence of a hypertrophied first phalanx of pedal digit I in *Enantiophoenix* are apomorphies of avisauridae *sensu* Chiappe (1993). This clade comprises Late Cretaceous forms from North America (*Avisaurus*, Brett-Surman & Paul, 1985) and South America (*Soroavisaurus* Chiappe, 1993; *Neuquenornis* Chiappe & Calvo, 1994) and is closely related with the Early Cretaceous *Concornis* from Spain (Sanz *et al.*, 1995). Our study also showed that the Late Cretaceous *Halimornis* from North America is a member of the avisaurid lineage. It is more derived than *Enantiophoenix* on the basis of the presence of a longitudinally grooved costal surface of the scapula, a character condition shared with *Neuquenornis* and absent in the Lebanese form. Given the absence of tarsometatarsus in the currently known specimen of *Halimornis*, it cannot be determined if it shares with avisaurids (*sensu* Chiappe, 1993) their derived tarsometatarsal morphology (address absence of tarsometatarsus in this specimen and the fact that avisauridae is based entirely on tarsometatarsal morphology – therefore *halimornis*' assignment to this family is very interesting)

Enantiophoenix bridges several gaps in the evolutionary history of enantiornithines. It is the first undisputable enantiornithine from the African Plate (Dalla Vecchia & Chiappe, 2002), the oldest known Late Cretaceous enantiornithine and the easternmost member of the avisaurid lineage, placed geographically between the more derived forms from western continents and the closest sister-taxa of Avisauridae, from Eastern Asia (*Sinornis*, *Eoenantiornis*, the lineage leading to *Longipteryx*, and the lineage leading to *Gobipteryx*). On the basis of the known fossil record, Avisauridae is a clade of exclusively non-Asian enantiornithines. The oldest known record of avisaurids is *Concornis*, from the Barremian of Spain (Sanz & Buscalioni, 1992). According to the phylogenetic framework depicted in the MPT reported here, we postulate the presence of at least four avisaurid lineages (*sensu* Norell, 1993) in the Barremian (*Concornis* itself and the lineages leading respectively to *Enantiophoenix*, *Halimornis* and the node “*Neuquenornis* + *Soroavisaurus*”; fig. 5). Given that *Concornis* is coeval with the rich Chinese avifaunas from the Jehol Biota (Zhou & Zhang, 2006), it is noteworthy that no Jehol enantiornithines included in our phylogenetic analysis are found to be members of Avisauridae. This observation may indicate the presence of regionalism among enantiornithines, and that avisaurids were restricted to Western continents. Future discovery of Asian avisaurids may falsify this hypothesis. Interestingly, Walker *et al.* (2007) suggest the presence of enantiornithine taxa with distributions spanning Europe, North and South America.

Although a detailed investigation of ornithothoracine interrelationships is beyond the scope of this study, we note that the phylogenetic positions of some taxa resulted in our MPT must be considered as tentative, pending a more detailed analysis of the taxa considered. In particular, the position of *Dalingheornis* (Zhang *et al.*, 2006) intermediate between the more derived enantiornithines and more basal forms, may be affected by the immaturity of the holotype specimen of this taxon (see Tykoski, 2005, for a detailed discussion of the effect of using OTUs based on immature specimens). The purported enantiornithine *Aberratiodontus* (Gong *et al.*, 2004) is resolved inside the euornithine clade, closer to *Yanornis* than to modern birds (see Tab. 1). This hypothesis has been mentioned recently (Zhou *et al.*, in press) and needs to reconsider at least five non-euornithine plesiomorphic features described in the holotype of *Aberratiodontus* (Gong *et al.*, 2004) as secondarily acquired reversals. Nevertheless, constraining *Aberratiodontus* to be an enantiornithine results in a topology that is 12 steps longer (and thus is significantly less

parsimonious) than the MPT. The exclusion of *Aberratiodontus* from our analysis does not alter the interrelationships among the other ingroup taxa.

The weak support among enantiornithines is probably due to the strong similarity of the postcranial skeletons of these birds and to the fragmentary nature of most of the taxa included in the analysis (Lamanna *et al.*, 2006). The weakness of the enantiornithine relationships is a common feature among avialan phylogenies (see Clarke & Norell, 2002; Sereno *et al.*, 2002), therefore, we remark that the inferences proposed in our study have to be considered as a preliminary attempt, subject to further revision of the enantiornithine fossil record.

Conclusions

This study demonstrates that the avian specimen MSNM V3882 is diagnosable by a unique combination of characters and two autapomorphies. The inclusion of *Enantiophoenix electrophyla*, gen. et sp. nov., in an analysis of basal avialan phylogeny supports the preliminary hypothesis of Dalla Vecchia & Chiappe (2002). In addition, it is shown that this bird is a basal member of a clade of enantiornithines, here called Avisauridae, widespread in North America, Europe and Gondwana. Although the results of the phylogenetic analysis discussed here is a useful initial test concerning the relationships of this Lebanese taxon, we emphasize that more complete remains of *Enantiophoenix* would improve our knowledge of its morphology and phylogenetic relationships.

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References

- Brett-Surman M. K. & Paul G. S., 1985 – A new family of bird-like dinosaurs linking Laurasia and Gondwanaland. *Journal of Vertebrate Paleontology*, 5: 133-138.
- Chiappe L. M., 1993 – Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of northwestern Argentina. *American Museum Novitates*, 3083: 1-27.
- Chiappe L. M., 2001 – Phylogenetic relationships among basal birds. In: *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*. Gauthier J. & Gall L. F. (eds.). *Peabody Museum of Natural History*, New Haven, CT: 125-139.
- Chiappe L. M., 2002 – Basal bird phylogeny: problems and solutions. In: *Mesozoic Birds: Above the Heads of Dinosaurs*. Chiappe L. M. & Witmer L. M. (eds.). *University of California Press*, Berkeley: 448-472.

- Chiappe L. M. & Calvo J. O., 1994 – *Neuquenornis volans*, a new Enantiornithes (Aves) from the Upper Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, 14: 230-46.
- Chiappe L. M., Ji S. A., & Ji Q. & Norell M., 1999 – Anatomy and Systematics of the Confuciusornithidae (Aves) from the Mesozoic of Northeastern China. *Bulletin of the American Museum of Natural History*, 242: 1-89.
- Chiappe L. M., Norell M., & Clark J., 2001 – A New Skull of *Gobipteryx minuta* (Aves: Enantiornithes) from the Cretaceous of the Gobi Desert. *American Museum Novitates*, 3345: 1-15.
- Chiappe L. M. & Dyke G. J., 2002 – The Cretaceous radiation of birds. *Annual Reviews of Ecology and Systematics*, 33: 91-124.
- Chiappe L. M., Lamb J. P. Jr. & Ericson P. G. P., 2002 – An enantiornithine bird from the marine Upper Cretaceous of Alabama. *Journal of Vertebrate Paleontology*, 22: 169-173.
- Chiappe L. M., Suzuki S., Dyke G. J., Watabe M., Tsogtbaatar D. & Barsbold R., 2006 – A new enantiornithine bird from the Late Cretaceous of the Gobi Desert. *Journal of Systematic Palaeontology*, 4: 1-16.
- Chiappe L. M. & Walker C. A., 2002 – Skeletal morphology and systematics of the Cretaceous euenantiornithes (Ornithothoraces: Enantiornithes). In: *Mesozoic Birds: Above the Heads of Dinosaurs*. Chiappe L. M. & Witmer L. M. (eds.). *University of California Press*, Berkeley: 240-67.
- Chiappe L. M., Ji S.-A., & Ji Q., 2007 – Juvenile Birds from the Early Cretaceous of China: Implications for Enantiornithine Ontogeny. *American Museum Novitates*, 3594: 1-46.
- Clarke J. A. & Norell M. A., 2002 – The morphology and phylogenetic position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. *American Museum Novitates*, 3387: 1-46.
- Clarke J. A., Zhou Z., & Zhang F., 2006 – Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. *Journal of Anatomy*, 208: 287-308.
- Dalla Vecchia F. M. & Chiappe L. M., 2002 – First avian skeleton from the Mesozoic of Northern Gondwana. *Journal of Vertebrate Paleontology*, 22 (4): 856-860.
- Dalla Vecchia F. M. & Venturini S., 1999 – The middle Cenomanian Lagerstätte of al Nammoura (Kesrouâne Caza, N Lebanon). In: *Extended Abstracts 3rd International Symposium on Lithographic Limestones*. Renesto S. (ed.). *Rivista del Museo Civico di Scienze Naturali di Bergamo*, 20.
- Elzanowski A., 1974 – Preliminary note on the paleognathous birds from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica*, 30: 103-9.
- Gauthier J., 1986 – Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, 8: 1-55.
- Gauthier J. & de Queiroz K., 2001 – Feathered dinosaurs, flying dinosaurs, crown dinosaurs and the name “Aves”. In: *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*. Gauthier J. & Gall L. F. (eds.). *Peabody Museum of Natural History*, New Haven, CT: 7-41.
- Gong E., Hou L. & Wang L., 2004 – Enantiornithine bird with diapsidian skull and its dental development in the Early Cretaceous in Liaoning, China. *Acta Geologica Sinica*, 78: 1-7.

- Holtz T. R. Jr., Molnar R. E., & Currie P. J., 2004 – Basal Tetanurae. In: The Dinosauria, 2nd edition. Weishampel D. B., Dodson P. & Osmólska H. (eds.). *University of California Press*, Berkeley: 21-24.
- Hou L., Martin L. D., Zhou Z. & Feduccia A., 1999 – *Archaeopteryx* to opposite birds-missing link from the Mesozoic of China. *Vertebrata Palasiatica*, 37:88-95.
- Hou L., Chiappe L. M., Zhang F., & Chuong C.-M., 2004 – New Early Cretaceous fossil from China documents a novel trophic specialisation for Mesozoic birds. *Naturwissenschaften*, 91: 22-25.
- Kitching I. J., Forey P. L., Humphries C. J. & Williams D. M., 1998 – Cladistics. *Oxford University Press*, Oxford.
- Kurochkin E., 1996 – A new enantiornithid of the Mongolian Late Cretaceous, and a general appraisal of the Infraclass Enantiornithes (Aves). *Special Issue of the Russian Academy of Sciences*: 1-60.
- Lamanna M. C., You H.-L., Harris J. D., Chiappe L. M., Ji S.-A., Lü J.-C. & Ji Q., 2006 – A partial skeleton of an enantiornithine bird from the Early Cretaceous of northwestern China. *Acta Palaeontologica Polonica*, 51 (3): 423-434.
- Linné K. af, 1758 – Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima. *Holmiae, impensis direct. Laurentii Salvii*.
- Marsh O. C., 1881 – A new order of extinct Jurassic reptiles (Coeluria). *American Journal of Science*, Series 3, 21: 339-340.
- Nixon H. C. & Wheeler Q. D., 1990 – An amplification of the phylogenetic species concept. *Cladistics*, 6: 211-223.
- Norell M. A., 1993 – Tree-based approaches to understanding history: comments on ranks, rules, and the quality of fossil record. *American Journal of Science*, 293-A: 407-417.
- Norell M. A. & Makovicky P. J., 1997 – Important Features of the Dromaeosaurid Skeleton: Information from a New Specimen. *American Museum Novitates*, 3215: 1-28.
- Norell M. A. & Makovicky P. J., 1999 – Important Features of the Dromaeosaurid Skeleton II: Information from Newly Collected Specimens of *Velociraptor mongoliensis*. *American Museum Novitates*, 3282: 1-45.
- Owen R., 1842 – Report on British fossil reptiles. Part II. *Reports of the British Association for the Advancement of Science*, 11: 60-204.
- Sanz J. L. & Bonaparte J. F., 1992 – *Iberomesornis romerali*, a fossil small bird articulated skeleton from the early Cretaceous of Spain. *Proceedings of the II International Symposium on Avian Paleontology, Los Angeles, 1988*: 39-49.
- Sanz J. L. & Buscalioni A. D., 1992 – A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. *Paleontology*, 35 (4): 829-845.
- Sanz J. L., Chiappe L. M. & Buscalioni A. D., 1995 – The Osteology of *Concornis lacustris* (Aves: Enantiornithes) from the Lower Cretaceous of Spain and a Reexamination of its Phylogenetic Relationships. *American Museum Novitates*, 3133: 1-23.
- Sanz J. L., Chiappe, L. M., Perez-Moreno B. P., Buscalioni A. D., Moratalla J. J., Ortega F. & Poyato-Ariza F. J., 1996 – An Early Cretaceous bird from Spain and its implication for the evolution of avian flight. *Nature*, 382: 442-445.
- Sanz J. L., Chiappe L. M., Pérez-Moreno B. P., Moratalla J., Hernandez-Carrasquilla F., Buscalioni A. D., Ortega F., Poyato-Ariza F. J., RassKin-Gutman

- D., & Martinez-Delclos X., 1997 – A nestling bird from the Early Cretaceous of Spain: implications for avian skull and neck evolution. *Science*, 276: 1543-1546.
- Sereno P. C., 2000 – *Iberomesornis romerali* (Aves, Ornithothoraces) reevaluted as an Early Cretaceous enantiornithine. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 215: 365-395.
- Sereno, P. C. & Rao C. G., 1992 – Early evolution of avian flight and perching: new evidence from Lower Cretaceous of China. *Science*, 255: 845-848.
- Sereno P. C., Rao C. G., & Li J. J., 2002 – *Sinornis santensis* (Aves: Enantiornithes) from the Early Cretaceous of northeastern China. In: Mesozoic Birds: Above the Heads of Dinosaurs. Chiappe L. M. & Witmer L. M. (eds.). *University of California Press*, Berkeley: 184-208.
- Swofford D. L., 2002 – PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. *Sinauer Associates*, Sunderland, Massachusetts.
- Tykoski R. S., 2005 – Anatomy, ontogeny and phylogeny of coelophysoid theropods. Ph.D. Thesis. *University of Texas*, Austin: 1-553.
- Walker C. A., 1981 – New subclass of birds from the Cretaceous of South America. *Nature*, 292: 51-3.
- Walker C. A., Buffetaut E. & Dyke G. J., 2007 – Large euenantiornithine birds from the Cretaceous of southern France, North America and Argentina. *Geological Magazine*, 144: 977-986.
- You H., O'Connor J., Chiappe L. M. & Quiang J., 2005 – A new fossil bird from the Early Cretaceous of Gansu Province, northwestern China. *Historical Biology*, 17: 7-14.
- Zhang F., Ericson P. G. P. & Zhou Z., 2004 – Description of a new enantiornithine bird from the Early Cretaceous of Hebei, northern China. *Canadian Journal of Earth Sciences*, 41: 1097-1107.
- Zhang F., Hou L., Hasegawa Y., O'Connor J., Martin L. D. & Chiappe L. M., 2006 – The first Mesozoic heterodactyl bird from China. *Acta Geologica Sinica*, 80 (5): 631-635.
- Zhang F. & Zhou Z., 2000 – A primitive enantiornithine bird and the origin of feathers. *Science*, 290: 1955-9.
- Zhang F., Zhou Z., Hou L. & Gu G., 2001 – Early diversification of birds-evidence from a new opposite bird. *Chinese Science Bulletin*, 45: 2650-2657.
- Zhou Z., 1995 – Discovery of a new enantiornithine bird from the Early Cretaceous of Liaoning, China. *Vertebrata Palasiatica*, 33 (2): 99 -113.
- Zhou Z., 2002 – A new and primitive enantiornithine bird from the Early Cretaceous of China. *Journal of Vertebrate Paleontology*, 22 (1): 49-57.
- Zhou Z., Clarke J., & Zhang F., in press – Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. *Journal of Anatomy*.
- Zhou Z. & Zhang F., 2006 – Mesozoic birds of China. A synoptic review. *Vertebrata Palasiatica*, 44 (1): 74-98.

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Appendix 1 - Character statements and character states used in the phylogenetic analysis

Appendice 1 - Definizione dei caratteri e degli stati dei caratteri usati nell'analisi filogenetica

1. Length of the skull in adult: between $4/5$ and $3/2$ of femoral length (0); less than $4/5$ of femoral length (1); more than $3/2$ of femoral length (2). The length of the skull is here defined as the distance from the rostro-ventral margin of premaxilla to the caudo-ventral margin of the mandibular condyles of the quadrate.
2. Length of the ventral margin of the premaxilla: between $5/2$ and $2/5$ (0); less than $2/5$ (1); more than $5/2$ (2); of the length of the ventral margin of the preantorbital ramus of the maxilla. The preantorbital ramus of the maxilla is here defined as the part of the maxilla between the rostralmost margin of the antorbital fossa and the latero-ventral margin of the maxilla-premaxilla suture.
3. Nasal process of premaxilla: rostro-caudally shortened, ending cranially to the level of the cranial border of the antorbital fossa (0); rostro-caudally elongate, reaching the level of the cranial border of the antorbital fossa (1); strongly rostro-caudally elongate, reaching the level of the caudal border of the antorbital fossa (2). Ordered. Modified from Clarke & Norell, 2002.
4. Maxillary process of premaxilla in lateral view: extremely broad and long, extending caudally from the caudal margin of the external naris for a distance greater than the rostro-caudal length of the external naris (0); reduced, bordering only the ventral margin of the external naris (1); process excluded from the ventral border of the external naris (2). Modified from Holtz *et al.*, 2004.
5. Premaxillary teeth: present (0); absent (1). Clarke & Norell, 2002.
6. Premaxillae in adult: unfused (0); fused (1). Clarke & Norell, 2002.
7. Maxillary fenestra: absent (0); present (1). Chiappe *et al.*, 1999.
8. Rostro-caudal length of the rostral ramus of the maxilla: subequal or shorter than $1/10$ of the ventral maxillary length (0); between $1/10$ and $1/4$ of the ventral maxillary length (1); more than $1/4$ of the ventral maxillary length (2). Ordered.
9. Rostral margin of the maxillary antorbital fossa: moderately developed, from $1/5$ to less than $2/5$ of the rostro-caudal length of the antorbital cavity (0); large, greater than $2/5$ of the rostro-caudal length of the antorbital cavity (1); greatly reduced in size, extending very little beyond the rim of the external antorbital fenestra (2). Modified from Holtz *et al.*, 2004.
10. Ventral margin of the antorbital fossa: extended for more than $1/3$ of the length of the antorbital fenestra and moderately shallow (0); extended for less than $1/3$ of the length of the antorbital fenestra and dorso-ventrally very shallow (1); extended for more than $1/3$ of the length of the antorbital fenestra and deeper than the ventral body of the maxilla (2). Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
11. Maxillary teeth: present (0); absent (1). Holtz *et al.*, 2004.
12. Maxillary tooth row: extends caudally to the rostral rim of orbit (0); ends ventrally to the ventral process of the lacrimal (1); ends ventrally to the antorbital fenestra (2); ends cranially to the antorbital fenestra (3). Ordered. Modified from Holtz *et al.*, 2004.
13. Length of the preantorbital maxillary length: less than (0); more than (1) $2/3$ of the length of the antorbital fossa. Modified from Holtz *et al.*, 2004.
14. Rostral ramus of the maxilla: absent, the rostro-dorsal surface of the maxilla forming a convex surface from the dorsal ramus to the ventral margin (0);

- present, with a dramatic change in the curvature of the rostradorsal surface of the maxilla rostral to the dorsal ramus, forming a concave surface shorter rostro-caudally than dorsoventrally (1); present, rostro-caudally as long as or longer than dorso-ventrally deep (2). Ordered. Modified from Holtz *et al.*, 2004.
15. Dorsal ramus of the maxilla in lateral view: present and caudally directed (0); strongly reduced or absent (1). Modified from Clarke & Norell, 2002.
 16. Nasal participation in the antorbital fossa: nasal entirely excluded (0); antorbital cavity reaches the nasomaxillary suture, but the lateral surface of the nasal is excluded from the antorbital cavity (1); lateral surface of the nasal participates in the antorbital fossa (2). Ordered. Modified from Holtz *et al.*, 2004.
 17. Subnarial process of the nasal: present (0); absent (1). Modified from Holtz *et al.*, 2004.
 18. Eminasals: contact but do not fuse (0); do not contact (separated by the premaxillary frontal processes) (1); fused (2). Modified from Holtz *et al.*, 2004; Clarke & Norell, 2002.
 19. Suborbital ramus of the jugal: significantly dorso-ventrally taller than medio-laterally wide (0); dorso-ventrally compressed, slender and rod-like (1). Modified from Holtz *et al.*, 2004.
 20. Postorbital process of the jugal: present and taller than half orbit (0); present but reduced, lower than the dorsal half of the orbit (1); absent (2); Ordered. Modified from Holtz *et al.*, 2004.
 21. Postorbital bar: closed (0); open (1). Clarke & Norell, 2002.
 22. Shape of the rostral half of the frontal in dorsal view: trapezoidal (0); triangular, without lateral processes (1); cranio-caudally reduced, the nasal articulation is placed close to plane of the lacrimal/prefrontal articulation (2). Modified from Holtz *et al.*, 2004.
 23. Length of the parietal: less than 3/4 of the frontal (0); subequal or more than 3/4 of the frontal (1). Modified from Holtz *et al.*, 2004.
 24. Parietals: unfused (0); fused (1). Modified from Holtz *et al.*, 2004.
 25. Fronto-parietal fusion: absent (0); present (1). Modified from Holtz *et al.*, 2004.
 26. Squamosal: unreduced and unossified to the neurocranial bones (0); reduced as a zygomatic process of the neurocranial bones (1). Modified from Chiappe, 2001.
 27. Quadrate recess: absent (0); present (1). Modified from Holtz *et al.*, 2004.
 28. Number of dorsal condyles of the quadrate: one (0); two (1). Modified from Clarke & Norell, 2002.
 29. Quadrate-quadratojugal articulation: overlapping (0); fused (1); quadratojugal “peg” in quadrate socket (2); quadrate “peg” in quadratojugal socket (3). Modified from Clarke & Norell, 2002.
 30. Paroccipital processes, dorso-ventral orientation: directed laterally (0); directed ventro-laterally (1); directed strongly ventro-laterally, with distal end below the level of the foramen magnum (2). Ordered. Modified from Holtz *et al.*, 2004.
 31. Dorso-ventral diameter of the dentary at mid-length: greater than 1/8 of dentary length (0); shorter than 1/8 of dentary length (1).
 32. Shape of the ventral margin of the dentary in lateral view: straight (0); concave (1); convex (1).
 33. Number of dentary teeth: between 11 and 24 (0); no more than 10 (1); more than 24 (2).
 34. Rostral fourth of the dentary: toothed (0); edentulous (1).
 35. Post-symphyseal dentary (with the exclusion of the part cited in the character

- 28): toothed for most of its length (0); toothed only in the rostral half (1); completely edentulous (2). Ordered.
36. Mesio-distal length of the dentary interdental septa: subequal to the mesio-distal length of the alveoli (0); reduced (teeth strongly packed) (1); greater than the mesio-distal length of the alveoli (2).
37. Caudo-dorsal process of the dentary: absent (0); present and shorter than 1/2 of the caudo-ventral process (1); present and longer than 1/2 of the caudo-ventral process (2). Ordered. Modified from Holtz *et al.*, 2004.
38. Mandibular symphysis: loose (0); tightly sutured (1); fused (2). Ordered. Modified from Clarke & Norell, 2002.
39. Rostro-dorsal corner of the dentary in lateral view: the rostral and the dorsal margins of the dentary meet at an angle broader than 60° (0); the rostral and the dorsal margins of the dentary meet describing an acuminate corner of less than 60° (1).
40. Dorso-ventral diameter of the external mandibular fenestra: greater than 1/3 of the greatest dorso-ventral diameter of the mandible (0); shorter than 1/3 of the greatest dorso-ventral diameter of the mandible (1); external mandibular fenestra absent (2). Modified from Holtz *et al.*, 2004.
41. Articular diverticula: absent or shallow (0); present and deep (1). Modified from Holtz *et al.*, 2004.
42. Axial epiphyses: absent (0); present as small ridges (1); present and overhanging the postzygapophyses (2). Ordered. Modified from Holtz *et al.*, 2004.
43. Caudal surface of the cervical centra: flat or slightly concave (0); deeply concave (1); saddle-shaped (2). Modified from Holtz *et al.*, 2004.
44. Ventral keel in cranial post-axial cervical centra: absent (0); present (1). Modified from Holtz *et al.*, 2004.
45. Post-axial cervical epiphyses: absent (0); present as low ridges (1); present and overhanging the postzygapophyses (2). Ordered. Modified from Holtz *et al.*, 2004.
46. Ventral processes cranial to the keel (hypapophyses) in cranial dorsals: absent or poorly developed (0); present and strongly developed, deeper dorso-ventrally than 1/3 of the depth of the cranial surface of the centrum (1). Modified from Holtz *et al.*, 2004.
47. Presence of pleurocoels in dorsal vertebrae: absent (0); present only in cranial dorsals (1); present in all dorsals (2). Ordered. Modified from Holtz *et al.*, 2004.
48. Cranial surface of the dorsal centra: quadrangular or subcircular, as tall as wide (0); medio-laterally wider than dorso-ventrally tall (1). Modified from Holtz *et al.*, 2004.
49. Dorsal vertebrae with ribs articulating with the sternum, one or more with prominent hypapophyses: (0) absent, (1) present. Following Clarke & Norell (2002) this character does not address the presence of hypapophyses on transitional vertebrae, or “cervico-dorsals”, that do not have associated ribs that articulate with the sternum (see character statement 46).
50. Dorsal vertebrae: without ossified connective tissue bridging the transverse processes (0); with ossified connective tissue bridging the transverse processes (1). Clarke & Norell, 2002.
51. Cranial surface of the caudalmost dorsal centra: flat (0); concave (1). Modified from Holtz *et al.*, 2004.
52. Position of the caudal dorsal parapophyses: cranio-ventral to diapophysis and ventral to prezygo-diapophyseal lamina (0); directly ventral to diapophysis, close to midpoint of the vertebra (1). Modified from Chiappe, 2001; Holtz *et al.*, 2004.

53. Uncinate processes of the dorsal ribs: unossified or absent (0); ossified (1). Modified from Holtz *et al.*, 2004.
54. Number of dorsal vertebrae: more than 11 (0); 11 (1); less than 11 (2). Ordered.
55. Gastralia: ossified (0); absent or unossified (1).
56. Number of sacral vertebrae (having the transverse processes in articulation with the medial wall of the iliac blades): two (0); three (1); four (2); five (3); six (4); seven (5); eight (6); nine (7); more than nine (8). Ordered. Modified from Clarke & Norell, 2002.
57. Medio-lateral width of the vertebral centra along the sacral series: all vertebrae subequal in width (0); medio-lateral width of the middle sacrals shorter than the width of the cranialmost and of the caudalmost vertebrae (1). Modified from Holtz *et al.*, 2004.
58. Sacral ribs in dorsal view: slender and well separated (0), forming a more or less continuous sheet of bone (1). Modified from Holtz *et al.*, 2004.
59. Number of caudal vertebrae: more than 47 (0); between 47 and 38 (1); between 37 and 28 (2); between 27 and 18 (3); less than 18 (4). Ordered. Modified from Chiappe, 2001; Holtz *et al.*, 2004.
60. Cranio-caudal length of the middle caudal centra: shorter than $3/2$ of the length of the proximal caudal centra (0); longer than $3/2$ of the length of the proximal caudal centra (1). Modified from Holtz *et al.*, 2004.
61. Pygostyle (distalmost caudal vertebrae fused): absent (0); present (1). Chiappe, 2001.
62. Length of the pygostyle: subequal or shorter than the sum of the lengths of the four distalmost free caudal vertebrae (0); longer than the sum of the lengths of the four distalmost free caudal vertebrae (1). Modified from Clarke & Norell, 2002.
63. Length of the tail: longer than $5/2$ of the proximo-distal length of the femur (0); shorter than $5/2$ of the proximo-distal length of the femur (1).
64. Scapula: shorter than humerus (0); longer than humerus (1).
65. Dorsal and ventral margins of the scapular blade in lateral/costal view: diverge caudally (0); subparallel for most of their length, diverge in the caudalmost part (1); subparallel, without distal expansion (2); converge caudally (3). Modified from Holtz *et al.*, 2004.
66. Scapulo-coracoid articulation in adult: sutured (0); mobile (1). Chiappe, 2001.
67. Scapular acromion in cranial view: dorso-ventrally deeper than costo-laterally wide (0); costo-laterally wider than deep (1). Chiappe & Walker, 2002.
68. Dorso-ventral diameter of the scapular acromion: taller than $4/5$ of the minimal dorso-ventral diameter of the scapular shaft (0); lower than $4/5$ of the minimum dorso-ventral diameter of the scapular shaft (1). Modified from Holtz *et al.*, 2004.
69. Longitudinal costal groove of the scapula: absent (0); present (1). Chiappe & Walker, 2002.
70. Lateral surface of the coracoid: lack a fossa/fenestra (0); excavated by a fossa (1); fenestrated (2). Modified from Holtz *et al.*, 2004.
71. Procoracoid process of the coracoid: absent (0); present (1). Chiappe, 2001.
72. Latero-distal process of the coracoid: absent (0); present (1). Modified from Clark & Norell, 2002.
73. Longitudinal bar of bone placed close to the medial margin of the coracoid: absent (0); present (1). Chiappe, 2001.

74. Acrocoracoid: absent or slightly developed (0); strongly developed process laterally directed (1); marked hooked process, medially directed (2). Modified from Clarke & Norell, 2002.
75. Supracoracoid nerve foramen: present on the central surface of the coracoid (0); present in a medial groove of the coracoid (1); absent (2). Modified from Chiappe, 2001.
76. Coracoidal articular facet for the scapula: flat or slightly concave (0); convex (1). Chiappe, 2001.
77. Coracoid in proximal view: cranio-caudally compressed (0); medio-laterally compressed (1). Chiappe *et al.*, 2006.
78. Ventral process of the coracoid: absent or present as a slightly developed lobular process (0); present and half-crescentic (1); present, proximally constricted and distally expanded (2). Modified from Holtz *et al.*, 2004.
79. Length of the scapulo-sternal axis of the coracoid: no more than 5/2 of its sternal width (0); between 5/2 and 3 times of its sternal width (1); more than 3 times its sternal width (2).
80. Latero-distal border of the coracoid: straight or slightly convex (0); broadly convex (1). Chiappe, 2001.
81. Proximal articular surface of the humerus: proximo-distally compressed, ellipsoidal (0); hemispherical (1); saddle-shaped, concave in the central part (2). Chiappe, 2001.
82. Proximo-distal length of the humeral deltopectoral crest: shorter than 1/3 of the proximo-distal length of the humerus (0); between 1/3 and 2/5 of the length of the humerus (1); longer than 2/5 of the length of the humerus (2). Ordered. Modified from Holtz *et al.*, 2004.
83. Distal margin of the deltopectoral crest of the humerus in lateral/medial view: forming a broad arch with the cranio-distal margin of the humeral shaft (0); forming an angle close to 90° with the cranio-distal margin of the shaft (1).
84. Deltopectoral crest with fenestra: absent (0); present (1).
85. Humeral bicipital crest: absent or without a ventral projection (0); prominent and cranially projected in ventral view (1). Chiappe, 2001.
86. Pneumotricipital fossa in proximal humerus: absent or poorly developed (0); large and rounded (1). Modified from Clarke & Norell, 2002.
87. Cranio-caudal diameter of the deltopectoral crest: subequal or greater than mid-shaft cranio-caudal diameter of the humerus (0); shorter than mid-shaft cranio-caudal diameter of the humerus (1). Modified from Holtz *et al.*, 2004.
88. Humerus shaft torsion (angle between the transverse axes of proximal and distal ends when viewed proximally/distally): absent, angle subequal or narrower than 25° (0); present, angle greater than 25° (1). Modified from Holtz *et al.*, 2004.
89. Groove placed proximally to the humeral proximo-ventral tubercle: absent or very shallow (0); present and deep (1); present as a low subtriangular depression (2). Modified from Clarke & Norell, 2002.
90. Latero-proximal fossa on the ulna for the insertion of the *Musculus brachialis*: absent or very shallow (0); present and marked (1). Chiappe & Walker, 2002.
91. Ulnar bicipital insertion: slightly developed scar (0); marked tubercle (1). Modified from Clarke & Norell, 2002.
92. Ratio of the proximo-distal length of the radius to the proximo-distal length of the femur: lower than 6/5 (0); equal or greater than 6/5 (1).
93. Proximo-distally elongate groove on the caudo-ventral margin of the radius:

- absent (0); present (1). Modified from Chiappe, 2001.
94. Medio-lateral mid-shaft diameter of the radius: greater than $3/5$ of the mid-shaft diameter of the ulna (0); shorter than $3/5$ of the mid-shaft diameter of the ulna (1).
 95. Distal end of the radius: unexpanded medially (0); expanded, bearing a medially flared articular surface (1). Modified from Chiappe *et al.*, 1999.
 96. Shape in dorsal view and position of the ulnare: discoidal ulnare placed distally to the ulna (0); subtriangular ulnare placed latero-distally to the ulna (1); “V”-shaped ulnare placed latero-distally to the ulna (2). Modified from Clarke & Norell, 2002.
 97. Proximo-distal length of metacarpal I: greater than $3/5$ of the length of metacarpal II (0); between $3/5$ and $2/5$ of the length of metacarpal II (1); between $2/5$ and $1/4$ of the length of metacarpal II (2); shorter than $1/4$ of the length of metacarpal II (3). Ordered. Modified from Holtz *et al.*, 2004.
 98. Distal condyles of metacarpal I: subequal in proximo-distal extension (0); lateral condyle medio-laterally broader and proximo-distally more elongate (1). Modified from Holtz *et al.*, 2004.
 99. Extensor process on the proximal end of metacarpal I: absent or present as a reduced tubercle (0); present as a prominent process (1). Modified from Chiappe, 2001.
 100. Medio-lateral diameter of mid-shaft of manual phalanx P-1I: between $1/2$ and $6/5$ of mid-shaft diameter of the radius (0); greater than $6/5$ of mid-shaft diameter of the radius (1); shorter than $1/2$ of mid-shaft diameter of the radius (2).
 101. Manual phalanx P-1I: proximo-distally subequal or shorter than manual phalanx P-1II (0); proximo-distally longer than manual phalanx P-1II (1).
 102. Manual phalanx P-1I: proximo-distally long no more than $3/2$ of metacarpal I (0); longer than $3/2$ of metacarpal I (1). Modified from Holtz *et al.*, 2004.
 103. Proximo-distal length of manual ungual I: subequal or shorter than the proximo-distal length of manual ungual II (0); greater than the proximo-distal length of manual ungual II (1).
 104. Metacarpal II and distal carpals: unfused (0); fused (1). Modified from Clarke & Norell, 2002.
 105. Proximo-distal length of manual digit I (sum of the lengths of metacarpal I and manual phalanges P-1I and P-2I): longer than the proximo-distal length of metacarpal II (0); subequal to the proximo-distal length of metacarpal II (1); shorter than the proximo-distal length of metacarpal II (2). Ordered.
 106. Proximo-distal length of manual digit I (P-1I + P-2I): between $3/5$ and $5/5$ of manual digit II (P-1II + P-2II + P-3II) (0); longer than manual digit II (1); shorter than $3/5$ of manual digit II (2).
 107. Proximo-distal length of manual phalanx P-1I: shorter than 5 times the medio-lateral width at mid-shaft of the same phalanx (0); longer than 5 times the medio-lateral width at mid-shaft of the same phalanx (1). Modified from Holtz *et al.*, 2004.
 108. Proximo-distal length of manual digit II (P-1II + P-2II + P-3II): shorter than $3/5$ of proximo-distal length of the humerus (0); between $3/5$ and $4/5$ of the humerus (1); longer than $4/5$ of the humerus (2). Ordered.
 109. Manual phalanx P-1II: cylindrical, only slightly compressed dorso-ventrally (0); strongly compressed dorso-ventrally (1); cylindrical, compressed dorso-ventrally along the lateral margin (presence of a lateral shelf) (2). Modified from Clarke & Norell, 2002.
 110. Manual phalanx P-2II: proximo-distally shorter than manual phalanx P-1II (0); subequal to manual phalanx P-1II (1); longer than manual phalanx P-1II (2). Ordered. Modified from Holtz *et al.*, 2004.

111. Proximo-distal length of manual ungual II: shorter than $3/5$ of manual phalanx P-2II (0); longer than $3/5$ of manual phalanx P-2II (1).
112. Articular surface for metacarpal II on metacarpal III: metacarpals articulate only along their proximal third (0); metacarpals II and III contact distally (1); metacarpals II and III fused distally (2). Modified from Holtz *et al.*, 2004.
113. Medio-lateral width of mid-shaft of metacarpal III: greater than $3/5$ of mid-shaft diameter of metacarpal II (0); between $3/5$ and $2/5$ of mid-shaft diameter of metacarpal II (1); narrower than $2/5$ of mid-shaft diameter of metacarpal II (2). Ordered. Modified from Holtz *et al.*, 2004.
114. Proximo-distal length of metacarpal III: longer than metacarpal II (0); between $4/4$ and $3/4$ of metacarpal II (1); shorter than $3/4$ of metacarpal II (2). Ordered. Modified from Holtz *et al.*, 2004.
115. Number of phalanges of manual digit III: four (0); three (1); two (2); one (3); none (4). Ordered. Modified from Chiappe, 2001.
116. Proximo-distal length of manual phalanx P-2III: longer than $4/5$ of manual phalanx P-1III (0); between $4/5$ and $1/2$ of manual phalanx P-1III (1); shorter than $1/2$ of manual phalanx P-1III (2). Ordered.
117. Shape of the manual unguals in lateral view: straight or slightly curved ventrally (0); curved ventrally (1); strongly curved ventrally, falciform (2). Ordered. Modified from Holtz *et al.*, 2004.
118. Sternal plates and ventral keel: sternal plates unfused, keel absent (0); sterna fused, keel absent (1); sterna fused, keel present on the caudal half of the ventral surface (2); sterna fused, keel present on almost the entire length of the sternum (3). Ordered. Modified from Clarke & Norell, 2002.
119. Cranio-caudal length of the sternum: shorter than $3/2$ of the medio-lateral width of its cranial half (0); subequal or more than $3/2$ of the medio-lateral width of its cranial half (1).
120. Prominent cranio-lateral processes of the sternum: absent (0); present and cranio-laterally projected (1). Modified from Clarke *et al.*, 2006.
121. Cranial margin of the paired sterna in ventral/dorsal view: concave or straight (0); convex, describing an obtuse cranial corner or a broad arch (1); convex, describing an acute cranial corner (2).
122. Caudo-lateral processes of the sternum: absent (0); present and short, do not reach the caudalmost extent of the caudo-median process of the sternum (1); present and elongate, reach the caudalmost extent of the caudo-median process of the sternum (2). Ordered. Modified from Clarke & Norell, 2002.
123. Medio-lateral expansion of distal end of the caudo-lateral process of the sternum: absent or reduced, narrower than $3/2$ of the medio-lateral diameter of the caudo-lateral process at mid-length (0); present and wider than $3/2$ of the medio-lateral diameter of the caudo-lateral process at mid-length (1).
124. Paired caudo-medial processes of the sternum: absent (0); present but cranio-caudally reduced (wider than long in ventral/dorsal view) (1); present and longer than wide (2); present and longer than wide, caudo-medially recurved and contacting the caudo-median process of the sternum (producing a pair of caudal fenestrae). Ordered. Modified from Clarke & Norell, 2002.
125. Single caudo-median process of the sternum: proximally broad, cranio-caudally long no more than $3/2$ of its proximal medio-lateral width (0); proximodistally elongate and narrow, without medio-lateral expansion of its distal end (1); proximodistally elongate and narrow, distally expanded (2). Ordered.

126. Lateral margin of the sternal plates: convex (0); broadly concave at mid-length (1).
127. Interclavicular angle: greater than 70° (0); lower than 70° (1). Chiappe, 2001.
128. Clavicles and hypocleidum: unfused clavicles (0); fused clavicles (furcula) without hypocleidum (1); furcula with a reduced hypocleidum, shorter than 1/3 of each clavicular ramus (2); furcula with a long hypocleidum, longer than 1/3 of each clavicular ramus (3). Ordered. Modified from Clarke & Norell, 2002.
129. Lateral longitudinal groove on the clavicular rami: absent, clavicular rami oval in cross section (0); present, clavicular rami “V” or “L”-shaped in cross section (1). Modified from Chiappe, 2001.
130. Ileo-ischial articulation: unossified in adult (0); ossified in adult (1).
131. Cranio-caudal length of the iliac blades: shorter than 3/5 of the proximo-distal length of the femur (0); longer than 3/5 of the length of the femur (1).
132. Ventralmost extent of the preacetabular blade: placed dorsally to the cranio-dorsal margin of the pubic peduncle of the ilium (0); placed ventrally to the cranio-dorsal margin of the pubic peduncle of the ilium but dorsally to the distal surface of the same peduncle (1); place at the same level of or more ventrally than the distal surface of the pubic peduncle of the ilium (2). Ordered.
133. Cranio-caudal diameter of the pubic peduncle of the ilium: shorter than the maximal cranio-caudal diameter of the acetabulum (0); subequal or shorter than the maximal cranio-caudal diameter of the acetabulum (1). Modified from Holtz *et al.*, 2004.
134. Cranio-caudal diameter of the ileo-ischial articulation: subequal to the cranio-caudal diameter of the ileo-pubic articulation (0); greater than the cranio-caudal diameter of the ileo-pubic articulation (1); shorter than the cranio-caudal diameter of the ileo-pubic articulation (2). Modified from Holtz *et al.*, 2004.
135. Cranio-caudal length of the preacetabular blade: shorter than the cranio-caudal length of the postacetabular blade (0); subequal to the cranio-caudal length of the postacetabular blade (1); longer than the cranio-caudal length of the postacetabular blade (2). Ordered. The caudalmost extent of the preacetabular blade is defined at the level of the cranio-dorsal margin of the pubic peduncle of the ilium; the cranialmost extent of the postacetabular blade is defined at the level of the caudo-dorsal margin of the ischial peduncle of the ilium. Modified from Holtz *et al.*, 2004.
136. Ventral margin of the postacetabular blade in lateral view: caudo-dorsally directed (0); subhorizontal (1); caudo-ventrally directed (2). Ordered.
137. Fossa for the origin of the *Musculus caudifemoralis brevis* on the ventral surface of the postacetabular blade: absent or very reduced cranio-caudally (0); present and cranio-caudally elongate (1). Modified from Holtz *et al.*, 2004.
138. Pubic shaft in lateral view: straight (0); cranially concave (1); caudally concave (2). Modified from Holtz *et al.*, 2004.
139. Cranio-caudal length of the caudal process of the pubic foot: process absent (0); process present but shorter than 1/5 of the proximo-distal length of the pubis (1); process present and long more than 1/5 but less than 1/3 of the proximo-distal length of the pubis (2); process present and longer than 1/3 of the proximo-distal length of the pubis (3). Ordered. Modified from Holtz *et al.*, 2004.
140. Distal contact between the hemipubic bones (pubic symphysis): present (0); absent (1). Chiappe, 2001.
141. Pubic shaft: cylindrical (0); medio-laterally compressed and laminar (1). Modified from Clarke & Norell, 2002.
142. Angle between the proximo-distal axis of the proximal half of the pubis and the

- cranial direction of the cranio-caudal axis of the sacral column: lower than 60° (pro-pubic condition); between 60° and 120° (mesopubic condition) (1); greater than 120° (opisthopubic condition) (2). Ordered. Modified from Holtz *et al.*, 2004.
143. Supplementary ischio-pubic contact placed distally to the acetabular region: absent (0); present (1). Modified from Holtz *et al.*, 2004.
144. Shape of the ischium in lateral/medial view: straight (0); caudo-dorsally concave at the level of the obturator process (1). Modified from Holtz *et al.*, 2004.
145. Proximo-distal length of the ischium: subequal or longer than the proximo-distal length of the pubis (0); between $5/5$ and $3/5$ of the proximo-distal length of the pubis (1); less than $3/5$ of the proximo-distal length of the pubis (2). Ordered. Modified from Holtz *et al.*, 2004.
146. Ischial proximo-dorsal process: absent (0); present as a low tubercle (1); present as an hypertrophied process, dorsally directed and distinct from the iliac peduncle of the ischium by a cleft (2). Ordered. Modified from Clarke & Norell, 2001; Holtz *et al.*, 2004.
147. Ischial medio-dorsal process: absent (0); present as a low tubercle (1); present as a proximo-distally elongate crest (2). Modified from Holtz *et al.*, 2004.
148. Femoral head: indistinct from the femoral shaft and the trochanteric region (0); cleft from shaft ("neck" present) but indistinct proximo-dorsally from the trochanteric region (1); cleft from shaft and from the trochanteric region (2). Ordered. Modified from Holtz *et al.*, 2004.
149. Proximalmost extent of the apex of the cranial trochanter: placed distally to the distal margin of the femoral head (0); placed proximally to the distal margin of the femoral head but distally to the apex of the greater trochanter (1); placed at the same level of the apex of the greater trochanter (2). Ordered. Modified from Holtz *et al.*, 2004.
150. Posterior trochanter of the femur: absent (0); present as a caudo-lateral mound-like eminence (1). Modified from Holtz *et al.*, 2004.
151. Cranial margin of the femur in distal view: straight or convex (0); moderately concave (1); deeply concave (2). Ordered. Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
152. Femoral caudo-distal fossa (flexor fossa): caudally opened and wider than half the medio-lateral diameter of the tibial condyle of the femur (0); narrower than half the medio-lateral diameter of the tibial condyle of the femur or closed off caudo-distally by contact between the distal condyles (1). Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
153. Caudal projection of the latero-distal margin of the femur: absent or slightly developed (0); marked (1). Chiappe, 2001.
154. Cranio-caudal diameter of the proximal surface of the tibia: between $6/5$ and $9/5$ of the medio-lateral diameter of the same surface (0); longer than $9/5$ of the maximal medio-lateral diameter of the same surface (1); long no more than $6/5$ of the maximal medio-lateral diameter of the same surface (2).
155. Number of cnemial crests: none (0); one (1); two (2). Ordered. Modified from Clarke & Norell, 2002.
156. Medio-lateral width of the intercondylar groove of the tibiotarsus: broader than $1/3$ of the medio-lateral width of the distal surface of the tibiotarsus (0); narrower than $1/3$ of the medio-lateral width of the distal surface of the tibiotarsus (1). Modified from Chiappe, 2001.
157. Complete fusion of the tibiotarsus in adult: absent, proximal tarsals and tibia unfused, sutures clearly visible (0); present, astragalo-calcaneum fused to the

- tibia (1). Modified from Chiappe, 2001.
158. Extensor canal on the cranio-distal surface of the tibiotarsus: absent (0); present (1). Chiappe, 2001.
159. Contact between fibula and calcaneum: present (0); absent, fibula longer than 1/2 of the tibia (1); absent, fibula long no more than 1/2 of the tibia (2). Ordered. Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
160. Ratio of the proximo-distal length of the tibia to the proximo-distal length of the femur: lower than 1; between 1 and 6/5 (1); greater than 6/5 (2). Ordered.
161. Metatarsals II, III and IV: unfused (0); proximally fused (1); almost completely fused (2). Ordered. Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
162. Metatarsal proximal vascular foramen/foramina: absent (0); present (1). Modified from Clarke & Norell, 2002.
163. Plantar expansion of the proximal surface of the tarsometatarsus (hypotarsus): absent (0); present (1). Modified from Chiappe, 2001.
164. Proximo-distal length of metatarsal II: shorter than the proximo-distal length of metatarsal III (0); subequal to the proximo-distal length of metatarsal III (1).
165. Distal end of metatarsal II strongly curved medially: absent (0); present (1). Chiappe, 1993.
166. Ratio of the proximo-distal length of metatarsal III to the proximo-distal length of the tibia: lower than 1/2 (0); between 1/2 and 2/3 (1); greater than 2/3 (2). Ordered.
167. Proximal tubercle on the extensor surface of metatarsal II: absent (0); present (1). Modified from Chiappe, 2001.
168. Position of the insertion of the *Musculus tibialis cranialis* on the proximal end of metatarsal II: placed in the middle of the extensor surface (0); close to the lateral margin (1); close to the medial margin (2).
169. Distal articular surface of metatarsal II: flat or slightly concave (0); markedly concave, with distinct extensor groove (1). Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
170. Proximal half of metatarsal III: unpinched mediolaterally (0); proximally pinched (1); strongly pinched proximally and through midshaft (2). Ordered. Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
171. Proximal surface of metatarsal III: subequal or greater than the proximal surface of both metatarsals II and IV (0); less developed than the proximal surface of both metatarsals II and IV or absent (1). Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
172. Extensor border of the proximal surface of metatarsal III: placed at the same level of the extensor surfaces of metatarsals II and IV (0); placed more plantarly than the extensor surfaces of metatarsals II and IV (1); placed less plantarly than the extensor surfaces of metatarsals II and IV (2). Modified from Chiappe, 2001.
173. Distal articular surface of metatarsal III: flat or slightly concave (0); markedly concave, with distinct extensor groove (1). Modified from Clarke & Norell, 2002; Holtz *et al.*, 2004.
174. Plantar projection of the medial distal condyle of metatarsal III in distal view: comparable to the plantar projection of the lateral condyle of the same metatarsal (0); more marked than the plantar projection of the lateral condyle of the same metatarsal (1). Chiappe, 1993.
175. Medio-lateral diameter of the distal articular surface of metatarsal III: subequal or broader than the medio-lateral diameter of the distal articular surface of

- metatarsal II (0); narrower than the medio-lateral diameter of the distal articular surface of metatarsal II (1). Modified from Chiappe, 1993.
176. Medio-lateral diameter of metatarsal IV at mid-length: between $2/3$ and $6/5$ of the medio-lateral diameter of metatarsal III at mid-length (0); narrower than $2/3$ of the medio-lateral diameter of metatarsal III at mid-length (1); broader than $6/5$ of the medio-lateral diameter of metatarsal III at mid-length (2). Modified from Chiappe, 1993.
 177. Proximo-distal length of metatarsal IV: greater than the proximo-distal length of metatarsal III (0); subequal to the proximo-distal length of metatarsal III (1); shorter than the proximo-distal length of metatarsal III (2). Ordered.
 178. Length of pedal digit IV: longer than pedal digit II (0); subequal to pedal digit II (1).
 179. Medio-lateral diameter of the distal articular surface of metatarsal IV: subequal or broader than $3/5$ of the medio-lateral diameter of the distal articular surface of metatarsal III (0); narrower than $3/5$ of the medio-lateral diameter of the distal articular surface of metatarsal III (1). Modified from Chiappe, 1993.
 180. Shape of metatarsal I in medial view: straight or slightly caudo-medially concave (0); "J"-shaped (1). Chiappe, 1993.
 181. Metatarsal I: placed medially to metatarsal II (0); placed medio-plantarly or fully plantarly to metatarsal II (1). Modified from Chiappe, 2001.
 182. Fossa on the plantar distal surface of the second metatarsal for the first metatarsal: absent (0); present (1). Clarke & Norell, 2002.
 183. Proximo-distal length of pedal phalanx P-1I: longer than $3/4$ of the proximo-distal length of pedal phalanx P-1III (0); long no more than $3/4$ of the proximo-distal length of pedal phalanx P-1III (1).
 184. Position of metatarsal I: placed in the proximal half of metatarsal II, its proximal surface reaches the ankle joint (0); placed in the proximal half of metatarsal II, its proximal surface is distally to the ankle joint (1); placed in the distal half of metatarsal II, its distal surface is proximally to the level of the distal surface of metatarsal II (2); placed in the distal half of metatarsal II, its distal surface is at the level of the distal surface of metatarsal II (3). Ordered. Modified from Holtz *et al.*, 2004.
 185. Proximo-distal length of pedal ungual I: subequal to the proximo-distal lengths of pedal unguals III or IV (0); significantly shorter than the proximo-distal lengths of pedal unguals III or IV (1); significantly greater than the proximo-distal lengths of pedal unguals III or IV (2).
 186. Ratio of the proximo-distal length of pedal phalanx P-2II to the proximo-distal length of pedal phalanx P-1II: lower than $3/4$ (0); between $3/4$ and 1 (1); greater than 1 (2). Ordered.
 187. Penultimate phalanges of pedal digit III and IV: are the shortest non-ungual phalanges of their digits (0); are subequal or longer than the remaining non-ungual phalanges of their digits (1).
 188. Proximo-distal length of pedal phalanx P-1IV: subequal or longer than the proximo-distal length of pedal phalanx P-1II (0); shorter than the proximo-distal length of pedal phalanx P-1II (1).
 189. Pedal unguals III and IV: straight or weakly curved (0); strongly ventrally curved (1).
 190. Metatarsal V: present (0); absent or unossified (1). Modified from Chiappe, 2001.
 191. Alular feathers: absent (0); present (1). Chiappe, 2001.
 192. Pair of elongate ribbon-like caudal feathers: absent (0); present (1).

Appendix 2 - Data matrix

Character states 0-8 for the 192 character statements used in this study are described in Appendix 1. “?” is either not preserved, unknown or inapplicable. Uncertainties (due to polymorphism or intermediate character states) are marked with letters: a = 0/1; b = 1/2; c = 2/3; d = 3/4; e = 4/5; f = 5/6; g = 6/7; m = 0/2; n = 0/3; s = 1/3.

Appendice 2 - Matrice dei dati

Le condizioni dei caratteri 0 – 8 per i 192 caratteri utilizzati in questo studio sono descritti in Appendice 1. “?” indica caratteri non preservati, sconosciuti od inapplicabili. Incertezze nelle codifiche (dovute a polimorfismo o a condizioni intermedie) sono espresse con lettere: a = 0/1; b = 1/2; c = 2/3; d = 3/4; e = 4/5; f = 5/6; g = 6/7; m = 0/2; n = 0/3; s = 1/3.

Input data matrix:

	1111111111222222222233333333333444444444455555555556
Taxon/Char.	123456789012345678901234567890123456789012345678901234567890
<i>Archaeopteryx</i>	00010011100200011001000000100110000200020?0110??00?000030031
<i>Jeholornis</i>	0?????????1???00???????0?0?0?0110?20b020?0???1????0?0?40031
<i>Aberratiodontus</i>	00b?0??2??0c?????12?????????1000000?0???????b?????????????
<i>Apsaravis</i>	0?????????????????1?????????1??00?12?22?0??2?0??????0?2?80040
<i>Archaeorhynchus</i>	0?211111121?00?b??12?????000?00?12?0?1?1?????????????1?05?04?
<i>Avisaurus</i>	???
<i>Boluochia</i>	??211?????????????????????????????????102?????????????????????
CAGS-IG-02-0901	???
CAGS-IG-04-CM-007	???
<i>Concornis</i>	???010???????
<i>Confuciusornis</i>	00211112111?12021101021??0012?00?12?11100?01?0b1?0001005?040
<i>Dalingheornis</i>	0?1?0?????0c???1?6??30
<i>Elsornis</i>	???01101???0???????
<i>Eoalulavis</i>	???011?????10?0?????
<i>Eocathayornis</i>	00110?????????001???b?10???000?00??????1?????????????10???????
<i>Eoenantiornis</i>	02110?12??02020101?????11?????0010?200?????????????????1?0?????
<i>Gansus</i>	???0??1??10?00218214?
<i>Gobipteryx</i>	?0211102?01?120101?????????????0??12?021?0??0?????????????7????
<i>Halimornis</i>	???20??01?????????
<i>Hongshanornis</i>	022?1??2??1??2?????121?????????10????0?1?????????????1?0???4?
<i>Iberomesornis</i>	???0??10???00010???30
<i>Ichthyornis</i>	2?2011????0?????1?????111111?10m0010002110001201100???8214?
<i>Longipteryx</i>	2???0??2??1?????????????????????11102??0?????0?????????1?06??4?
<i>Longirostravis</i>	2???0??2??1??2?????????????????111020??1?????????????1?0f004?
MSNM V3882	???
Neornithes	0?221102??1???12?1121?11111120???12?a2??1021012?111012182140
<i>Neuquenornis</i>	?????????????????????????????0?0?????????????????????2?????1?????????
<i>Patagopteryx</i>	?????????????????????????10??1112?????????0???0?21a1??0?1001?70???
<i>Protopteryx</i>	0?1?011???1?????????????????000?0102?????????????????00105??4?
<i>Sapeornis</i>	001100?1??031???1??10?1?????????01?12?1012??0??????0?0?00500d0
<i>Sinornis</i>	0012011201030???00?????1??00??00102?001???????b???01???6004?

<i>Soroavisaurus</i>	??
<i>Vescornis</i>	00????20?0c120????2?????????1010120?????0?????????0600??
<i>Vorona</i>	??
<i>Yanornis</i>	0?2101?2??0c10?????1????0??1??1000a?b0?????????????0??0700??
<i>Yixianornis</i>	0?21?1?????????????1210?00??12??0?01?20????0??1???0?012070??

Input data matrix (continued):

	11111111111111111111
	666666666777777777788888888889999999999000000000011111111112
Taxon/Char.	123456789012345678901234567890123456789012345678901234567890
<i>Archaeopteryx</i>	0?002?001000101000110010000010000000210011m00012021001011?00
<i>Jeholornis</i>	0?0021?01?2010?0??2110100??0?0001011c?02110a00112110010210??
<i>Aberratiodontus</i>	1?103???????1????2???2?0??0????1?1????????????????????211
<i>Apsaravis</i>	1011310?1?10?1110?2201?00110?1110011321????1????1???2????3??
<i>Archaeorhynchus</i>	?0103???1???101???2101100??0????101?3?0??????????11?021???300
<i>Avisaurus</i>	??
<i>Boluochia</i>	11??20?
CAGS-IG-02-0901	???0?1101??0??????2211100?00?1?1?0113?00???1???0101?103?1???
CAGS-IG-04-CM-007	??
<i>Concornis</i>	???0311???10011?1122121001101121??1?3??20??12m10000?a03?1200
<i>Confuciusornis</i>	1110b00110000012?0210021100011010010210211110012210011001100
<i>Dalingheornis</i>	??102??????????????211???????????1?0??????????0?0?b?000?????1
<i>Elsornis</i>	???0c11010100012102112000011?011?11?3?0????1???????20????21?
<i>Eoalulavis</i>	???0310?1?10011f11221210?1001111?1113??2?10?12?021?0003?1210
<i>Eocathayornis</i>	???031??10000?1?1?2112100110?????1113??2010122?02000?0221200
<i>Eoenantiornis</i>	1?10c?1?1?1?11?12100100??0???101113?02110?12102010103?1c00
<i>Gansus</i>	101031?01?0110120?2101100??0?1111?11321201012210100221?0310
<i>Gobipteryx</i>	11??310?1?10011111220m??0??01111?1??3????????????????000?????
<i>Halimornis</i>	11???11?01??????11???2??011???2????????????????????????????
<i>Hongshanornis</i>	10102??01??10?????2101100??0????0?1?3?0211010m11110011221?00
<i>Iberomesornis</i>	111031?0??100?11??2100?0?0????0?101????????????????????2??
<i>Ichthyornis</i>	1010310?1?0110200?210110001001111012321200?1220210?2213??311
<i>Longipteryx</i>	1110c1?????00???112?021001?0??1?1011c?02010012?02110102212??
<i>Longirostravis</i>	1110c?1?1??00?????2102100??0????1?1?c?0????1???????0?03??b00
MSNM V3882	????3???101001?1?1221????????????????????????????????????
<i>Neornithes</i>	1010310000011020002b01?000110111?012321200?1220010?2213?031?
<i>Neuquenornis</i>	???0c1?0?1100111??221?100?100???1111??0?0??1???????000???3??
<i>Patagopteryx</i>	???1310?11000012002?001000?000?1?00????????1???a01?201???1??
<i>Protopteryx</i>	111031??1??11?120?21001001?0??0?101?3??211000010221010221200
<i>Sapeornis</i>	111030?11??0?010??1100011000?10010103?021101001a?11111201???
<i>Sinornis</i>	1110c110101001111122121001101???11113?02010a2210200010c?1200
<i>Soroavisaurus</i>	??
<i>Vescornis</i>	1??0c1?010?00?????2212100110??0101113?02010?22102000003?0200
<i>Vorona</i>	??
<i>Yanornis</i>	10?031??1?01101?0?21012000?0?1111011c002110010101102213?1311
<i>Yixianornis</i>	101031?01?0110100?2101200??0?1?100013012111112101102213?13??

Input data matrix (continued):

	111111111111
	888888888999
Taxon/Char.	123456789012
<i>Archaeopteryx</i>	0?1202110000
<i>Jeholornis</i>	0?0302111000
<i>Aberratiodontus</i>	??1??1?101??
<i>Apsaravis</i>	?0???a0001??
<i>Archaeorhynchus</i>	?????0?0?1?
<i>Avisaurus</i>	?0??2???????
<i>Bohuochia</i>	????0???11??
CAGS-IG-02-0901	????????????
CAGS-IG-04-CM-007	1?03021101??
<i>Concornis</i>	1?03221111??
<i>Confuciusornis</i>	100302111001
<i>Dalingheornis</i>	1?030?1?1?1?
<i>Elsornis</i>	?????????0???
<i>Eoalulavis</i>	???????????1?
<i>Eocathayornis</i>	?????????????
<i>Eoenantiornis</i>	1?0302??0110
<i>Gansus</i>	1?12?10001??
<i>Gobipteryx</i>	10?2????01??
<i>Halimornis</i>	?????????????
<i>Hongshanornis</i>	??02?1110110
<i>Iberomesornis</i>	1?0302110???
<i>Ichthyornis</i>	?1????????1??
<i>Longipteryx</i>	1?030????1??
<i>Longirostravis</i>	??03???????1
MSNM V3882	1???2???1???
<i>Neornithes</i>	11?3????0110
<i>Neuquenornis</i>	100322???????
<i>Patagopteryx</i>	00?20a0??1??
<i>Protopteryx</i>	1??302110011
<i>Sapeornis</i>	1?020??110??
<i>Sinornis</i>	1?03021111??
<i>Soroavisaurus</i>	1??22???????
<i>Vescornis</i>	1?03021111??
<i>Vorona</i>	?0???????0??
<i>Yanornis</i>	??13010101??
<i>Yixianornis</i>	?012?10101?0